5

22102142212

Compliments of
C. Judson Herrick

ARTICLES FROM

"THE REFERENCE HANDBOOK OF THE MEDICAL SCIENCES"

(WILLIAM WOOD & CO., NEW YORK, THIRD EDITION)

BY

C. JUDSON HERRICK

Professor of Neurology, University of Chicago

I

OLFACTORY NERVE

From Volume VI, 1916, Pages 865–70

II

PHRENIC NERVE

From Volume VII, 1917, Pages 187–88

III

SPINAL CORD AND SPINAL NERVES

From Volume VII, 1917, Pages 828–55

328032 / 32776

WELLCOME LIBRARY INSTITUTE

WELLCOME INSTITUTE LIBRARY
Coll. welMOmec
Call No. WL
K54555

or even wholly substituted, and many other seed oils have been more or less employed as adulterants.

Sweet almond oil has, strictly speaking, no medicinal properties, being used wholly for its nutritive, demulcent and mechanical properties. It is an ingredient of the official rose-water ointment.

HENRY H. RUSBY.

Olfactory Nerve.—I. ANATOMY.—The olfactory nerve exhibits many structural peculiarities, some of which have been interpreted as primitive, while others give evidence of a high degree of specialization. Our description will begin with a brief account of the peripheral and central relations of the human nerve, which is in a reduced condition, after which the structure of these organs in some lower vertebrates where they are better developed will be taken up and some phylogenetic and physiological considerations will be discussed.

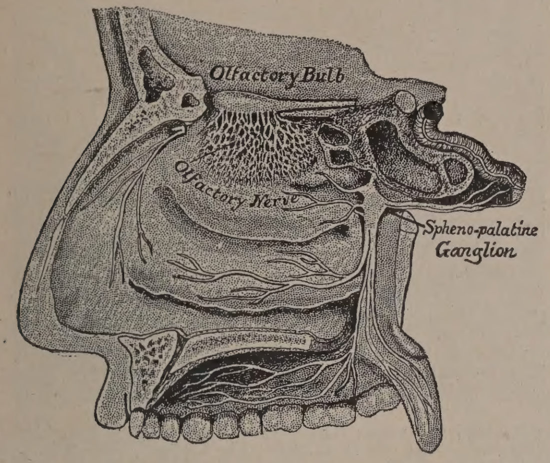

FIG. 4171.—The Right Olfactory Nerve on the Outer Wall of the Nasal Fossa. (Adapted from Hirschfeld.)

The general relations of the olfactory nerve of man to the nose and to the primary cerebral centers are seen in Fig. 4171. The respiratory region of the nasal passages is lined with ciliated epithelium. The olfactory region is a circumscribed area in the narrow upper part of the nasal sinus, partly on the superior turbinated bone and partly on the nasal septum adjacent. This area can be distinguished in the fresh preparation by its brownish-yellow color, the surrounding respiratory membrane having a more reddish appearance.

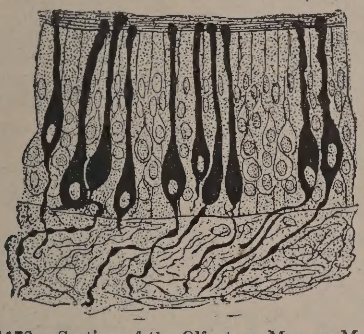

FIG. 4172.—Section of the Olfactory Mucous Membrane. (After von Brunn.) The specific olfactory cells are in black.

The sustentacular cells of the specific olfactory region (Schneiderian membrane) are of the pseudostratified type and, in contrast with those of the respiratory region, they are non-ciliated. The specific olfactory cells are narrowly spindle shaped (Fig. 4172) and each terminates peripherally in a blunt cone bearing several olfactory hairs which project outward into the mucus with which this membrane is continually bathed. These hairs are apparently the olfactory receptors, being stimulated chemically by substances dissolved in the nasal mucus. In fishes Jagodowski has found that each of these cells is provided with a long thread-like filament which projects outward into the mucus of the nose and which may be more than twice the length of the cell body from which it springs.

The central end of each specific olfactory cell is prolonged into a nerve fiber. These fibers are non-medullated and are gathered into about twenty bundles, the fila olfactoria, which enter the cranium by separate apertures in the cribriform plate of the ethmoid bone. Upon entering the olfactory bulb which lies immediately adjacent, these fibers form tufts of terminal arborizations, termed glomeruli, where they enter into synaptic relations with dendrites of the mitral cells of the bulb; these mitral cells constitute the neurones of the second order in the central olfactory path (Fig. 4173).

Further consideration of the central relations of the olfactory nerve can best be deferred until after a summary of its comparative anatomy and embryology. In cyclostome embryos there is an ectodermal thickening near the anterior end of the head which invaginates and then divides into two pits. The posterior pit forms the glandular part of the hypophysis and the anterior pit the nasal fossa (Fig. 4174). In higher vertebrates the right and left nasal fossæ arise separately,

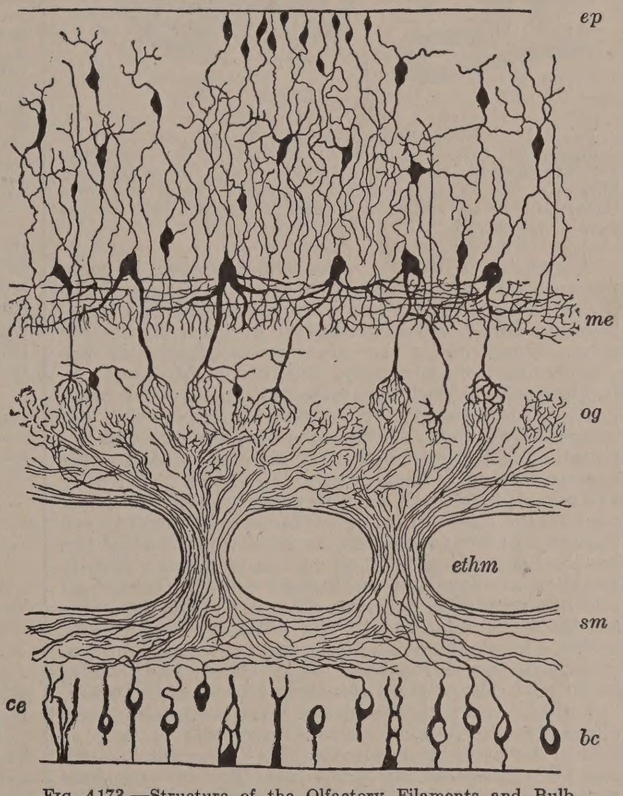

FIG. 4173.—Structure of the Olfactory Filaments and Bulb. (After Ramón y Cajal.) *bc*, Bipolar cells of the olfactory mucous membrane; *sm*, submucosa; *ethm*, cribriform plate of the ethmoid; *og*, olfactory glomeruli; *me*, mitral cells; *ep*, epithelium of the olfactory ventricle; *ec*, epithelial cells of the olfactory membrane.

each from an ectodermal placode, and the invaginated nasal pits come to lie on each side close to the anterior end of the fore-brain. The lateral evagination of the olfactory centers of the fore-brain is correlated with the invagination of the olfactory epithelium from the ectoderm, and throughout life these two parts are in close physiological and anatomical relations.

In some amphibians, reptiles, and mammals there is a peculiar diverticulum of the nasal sac, Jacobson's organ, or the vomeronasal organ, in the medioventral part of the nasal chamber. In some species this organ is large and it may communicate by a separate pore through the roof of the mouth with the buccal cavity. In man the organ is present, though rudimentary. The vomeronasal organ when well developed is lined with specific olfactory epithelium and a special slip of the olfactory nerve, the nervus vomeronasalis, supplies this part of the epithelium and may terminate in a specially differentiated part of the olfactory bulb, the formatio vomeronasalis of McCotter.

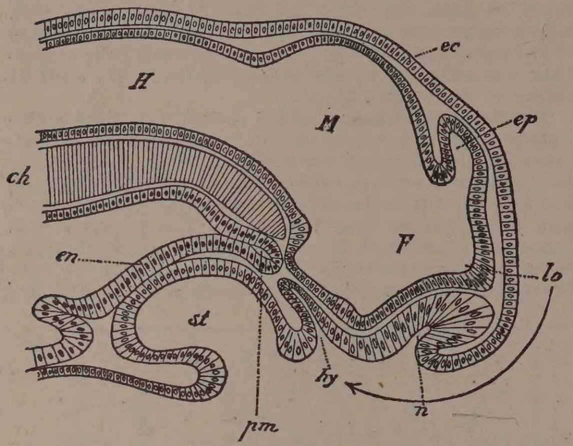

Fig. 4174.—Median Sagittal Section through the Head of Ammocœtes. (After von Kupffer.) *ch*, Notochord; *ec*, ectoderm; *en*, entoderm; *ep*, epiphysis; *F*, primary forebrain; *H*, primary hindbrain; *hy*, hypophyseal invagination; *lo*, lobus olfactorius impar; *M*, primary midbrain; *n*, nasal invagination; *pm*, pre-oral gut; *st*, stomodœum.

Associated with the vomeronasal nerve in some mammals is a very small nerve of fundamentally different type, the nervus terminalis. This is a ganglionated nerve which terminates peripherally in free arborizations under the olfactory membrane of the vomeronasal organ chiefly, and internally enters the brain quite behind the olfactory and vomeronasal bulbar formations. These fibers peripherally are mingled with those of the vomeronasal nerve and the ganglion cells from which they arise are scattered for a considerable distance along the nerve. Centrally the nervus terminalis separates from the vomeronasal nerve and enters the brain farther backward, apparently in the precommissural body in front of the anterior commissure. The nervus terminalis and its ganglion are found in the human embryo (Johnston) and in mammalian embryos generally. Fig. 4175 illustrates their relations to the olfactory organs and cerebral hemisphere in a fifteen-millimeter pig embryo. Here, as in the adult cat and dog, it clearly has nothing to do with the primary olfactory centers of the brain, but enters the precommissural body well behind the olfactory bulb. The nervus terminalis is present also in the adult human body. Its intracranial course has been described by Brookover (Fig. 4176) and its peripheral course by McCotter. It connects with the brain in the region of the olfactory trigone and peripherally it distributes in the nasal cavity to the septal mucosa anterior to the path of the vomeronasal nerves.

The first clear description of the nervus terminalis was that of Pinkus in 1894 for the lung-fish, Protopterus. About ten years later Locy in a series of important papers described this nerve in a number of selachians and gave it the name which it now bears, and it has since been described in representatives of most of the important groups of vertebrates. Its function is unknown, but is quite certainly different from that of the olfactory nerve, for, in the first place, peripherally it ends by free arborizations under the mucous membrane of the nose without connection with the specific olfactory cells, and in the second place, its central connections in the brain are far removed from those of the olfactory fibers in the olfactory bulb.

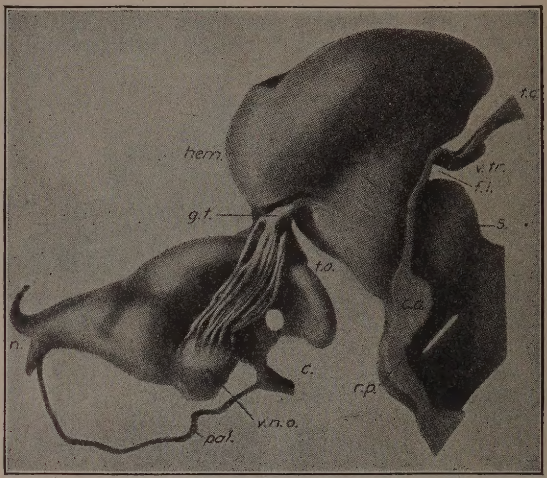

Fig. 4175.—Drawing of a Model of the Right Cerebral Hemisphere and Nasal Sac of a 15mm. Pig Embryo, Seen from the Medial Surface. The model includes the medial wall and frontal pole of the hemisphere. The groove in the hemisphere is the fissura prima of His. The root of the nervus terminalis is directed backward into the precommissural region. The olfactory nerve forms a dark background for the ganglion terminale in the drawing. It is at this point that olfactory fibers coming from the vomeronasal organ separate from the nervus terminalis fibers and enter the olfactory bulb. The two kinds of fibers run together in the bundles which go to the vomeronasal organ. (After Johnston.) *c.*, choana; *c.a.*, commissura anterior; *f.i.*, foramen interventriculare; *g.t.*, ganglion terminale; *hem.*, hemisphere; *n.*, narial opening; *pal.*, palate; *r.p.*, recessus preopticus; *s.*, corpus striatum; *t.c.*, tela chorioidea; *t.o.*, tuberculum olfactorium; *v.n.o.*, vomeronasal organ; *v.tr.*, velum transversum. (After Johnston, *Journal Comp. Neurology*, 1913.)

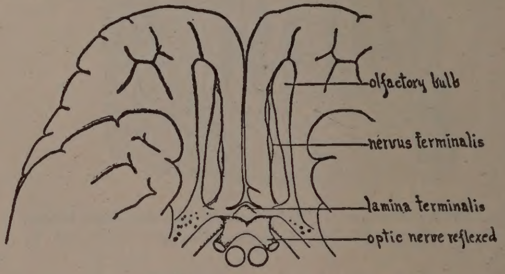

Fig. 4176.—Outline of the ventral surface of the adult human brain to show the position of the nervus terminalis. (After Brookover, *Journ. Comp. Neurology*, 1914.)

That the nervus terminalis is concerned with the general tactile sensations of the nasal cavity seems improbable from the fact that in vertebrates generally this region has an independent innervation for the tactile sense from the trigeminus nerve. This is true even in fishes, where the nervus terminalis attains its maximum development.

The details of the central connections of the nervus terminalis are not yet fully understood. Its fibers probably end by free arborizations in the precommissural body and septum and in the Amphibia also in the preoptic nucleus farther caudad. McKibben has traced fibers to this system in Necturus backward throughout the entire length of the hypothalamus and into the floor of the midbrain in the vicinity of the interpeduncular nucleus.

The exact mode of development of the olfactory nerve has been variously described, but the concurrent testimony of the best recent students supports the description of Wm. His, Jr., in 1889, that the olfactory nerve arises exclusively by inward growth from the olfactory placode.

The fibers of the olfactory and vomeronasal nerves arise as centrally directed processes of the specific olfactory cells of the Schneiderian membrane. These cells, therefore, constitute the cell bodies of the olfactory neurones of the first order, and are comparable with the spinal ganglion cells of the other sensory systems. These are the only sensory neurones found among the true vertebrates whose cell bodies are thus peripherally located (see *End-organs, Nervous*), though Dogiel has described similar sensory cells in the tentacles and adjacent parts of the skin in Amphioxus and analogous relations have long been known to occur in the skin of Lumbricus and other invertebrates.

In view of these facts, it has commonly been assumed that the olfactory apparatus represents the most primitive type of sense organ known among the vertebrates. But this conclusion by no means certainly follows, for the generalized nerves of the spinal type whose neurones develop from the neural crest, seem in some respects more primitive. And the giant ganglion cells which appear in the dorsal part of the spinal cord of lower vertebrates (chiefly as transient structures) and supply general sensibility to the skin represent perhaps a still more primitive condition. The two types of cutaneous nerves last mentioned are endowed with a very special chemical sensibility in all cases where they distribute to moist surfaces, as in the skin of fishes (Sheldon) and the mouth cavity of man. Furthermore, Landacre has shown that the specialized chemical receptors for taste, like those for smell, are differentiated from special ectodermal placodes. These placodes form an epibranchial series related to the gill clefts from which neuroblasts during early embryonic stages migrate inward to join other neuroblasts derived from the neural crest to form the mixed visceral sensory ganglia of the VII, IX, and X cerebral nerves. The general visceral sensory neurones of these ganglia are derived from the neural crest, like the generalized sensory nerves for tactile sensibility, while the more highly specialized gustatory component of these ganglia is derived from the placodes (see *Cranial Nerves*). If the olfactory placode belongs to the epibranchial series (as seems probable), it may be that the neurones of the olfactory nerve derived from it should be compared with the highly differentiated gustatory neurones of the VII, IX, and X nerves rather than with the more generalized components of these nerves derived from the neural crest. Johnston is of the opinion that the ganglion of the nervus terminalis is derived from the anterior end of the neural crest; but Brookover in fishes finds that these neurones migrate inward from the olfactory placode along with other cellular elements which go to form the sheath nuclei of the fibers of the olfactory nerve.

The problem of the functional and morphological relationships of the nervus terminalis must be solved before a complete understanding of the olfactory nerve itself is possible. It may be that the nervus terminalis is a remnant of a nerve of general chemical sensibility of the nose region, which has been largely supplanted by the more highly developed chemical receptors of the specific olfactory system. On the other hand, it may be a nerve of general visceral efferent type, the cells of the ganglion terminale being postganglionic sympathetic neurones.

The cerebral connections of the olfactory nerve are described in the article *Brain, Anatomy of*, and need not be here reviewed. In that discussion it is shown that the phylogenetic history and morphological interpretation of the vertebrate cerebral hemisphere are intimately related to the olfactory apparatus. The olfactory bulb was probably the first part of the hemisphere to be differentiated and its other parts were gradually elaborated under the physiological influence of ascending non-olfactory tracts adapted to bring the olfactory impulses into correlation with other sensory systems, particularly those of the exteroceptive type (cf. *End Organs, Nervous*). The most important of these primitive correlations are those concerned with feeding, viz., the olfactory-gustatory-tactile systems of reflexes concerned with the functions of the nose and lips, the muzzle-reflexes or "oral sense" complex of Edinger. Under the influence of these correlations a series of olfacto-gustatory and olfacto-visceral centers was elaborated on the medial side of the cerebral hemisphere and a series of olfacto-somatic centers on the lateral side. As a further differentiation from these basal reflex centers, the cerebral cortex was developed—the archipallium forming the margin of the cortex adjacent to the basal centers. The archipallium, or olfactory cortex, as the term is here employed, includes the pyriform lobe and uncus laterally and the hippocampus along the medial and posterior borders of the cortex. The non-olfactory cortex, or neopallium, is developed dorsally between the medial and lateral archipallial masses and above the corpus striatum.

II. Physiology.—The sense of smell in human beings, as compared with many of the lower animals, is very feebly developed, as will be made clear by even a cursory examination of the comparative anatomy and physiology of the organ. Animals are classified with reference to this sense as osmatic and anosmatic, and the former group is subdivided into macrosmatic and microsmatic divisions, depending upon whether the sense is highly developed or but feebly so. Man belongs to the microsmatic group, this sense playing a very subordinate rôle, either physiological or psychological, in our vital economy. Its unimportance is, however, more apparent than real and is to be explained, as Zwaardemaker points out, on psychological grounds.

As a matter of fact, olfactory sensations are always with us and our daily actions are profoundly influenced by them, though this influence is largely unrecognized as such. For these sensations are, in the case of human beings, intimately connected with the visceral and organic functions, and have a strong emotional content which obscures the process of ideation. This imperfect comprehension of olfactory impressions is reflected in our language, for our vocabulary of olfactory sensations is very limited and almost all borrowed from that of other senses. For our knowledge of the outer world we depend chiefly upon the other special senses, particularly sight. With the macrosmatic animals, on the other hand, the sense of smell is undoubtedly in some cases more potent in the elaboration of knowledge of the outer world than any other sense.

The physiology of the sense of smell is less perfectly known than that of any of the other special senses, and the same remark holds true of its psychology. While our knowledge of the anatomical arrangements of the paths of olfactory conduction to and within the brain has been greatly extended of late, we are yet ignorant of the means even by which the olfactory nerve termini are stimulated by the odorous substances. In particular, the physiological process underlying the difference between smell and taste is obscure. It is commonly stated that we taste substances in solution or in liquid form, while only gases are perceived by the sense of smell. While this is in general true, it nevertheless must be remembered that the odorous gases do not come into direct contact as such with the sensory end organs in the nose, either in fishes, where the nasal cavities are filled with water, or in air-breathing vertebrates, whose olfactory mucous membranes are always bathed with mucus in which the odorous substance must be dissolved before it can irritate the sensory endings. Again, some sapid substances, such as hydrochloric acid, are also solutions of gases, and some solids in a state of fine division seem to give rise to distinct olfactory impressions. The fact that when the nostrils are filled with water carrying an odorous substance in solution the odor cannot be perceived does not necessarily imply that the failure is due to the fact that the substance is in solution, but rather to an irritating effect of the liquid upon the olfactory organ. This is indicated by two facts: First, that all olfactory sensation may be temporarily enfeebled or even entirely abolished for some time after the close of the experiment; and second, that if normal salt solution instead of water be used as a solvent, then the dissolved substance can in some cases still be smelled.

Tyndall discovered that odorous vapors have a considerable capacity for absorbing heat, and that very minute quantities of the odorous substance in the air experimented upon would produce surprising effects. At the close of a table giving the absorptive powers of different odorous vapors, he remarks: "We find that the least energetic in the list produces thirty times the effect of air, while the most energetic produces one hundred and nine times the same effect." The significance of these facts is still obscure. We certainly are not able to affirm as yet, with Ramsay, that the sense of smell is excited by vibrations of a lower period than those which give rise to the sense of light or heat, though it may well be that characteristic molecular vibrations give to various substances their distinctive odors. But in any case these movements seem to be incapable of transference to the receptive sense organ by the medium of ethereal vibrations, and direct contact of the odorous particles with the nervous organ seems indispensable. The ultimate stimulus is probably electro-chemical—a matter of ions.

Olfactory sensations are aroused with difficulty or not at all by irritation of the peripheral end organ by thermal, electrical, mechanical, or other stimuli than the normal gaseous media, though tumors or other irritants of the central olfactory apparatus may call forth vivid sensations of smell. It is hardly true, as often stated, that air containing odorous particles must be in motion in order to stimulate the olfactory organ. The truth is that in ordinary respiration the air currents do not strike the sensory surface directly, and hence olfactory impressions are called forth by such particles only as diffuse themselves upward from the respiratory portion into the olfactory fossa, while in sniffing the direction of the air currents is altered so as to pass more directly over the specific sensory area.

We are not as yet able to give a natural classification of smells, nor have we any secure basis for such a classification. Even the division into agreeable and disagreeable is subject to so great variation from one individual to another that it would be of small value, even if it were admissible on other grounds. Accordingly, the names of smells are usually taken from the objects which give rise to them, with little attempt at classification or correlation of similars.

The number of smell qualities is very large. Some of those commonly recognized are compound, though authorities differ as to the extent to which such mixture is possible, or whether it is possible at all. If two distinct odors are mingled under experimental conditions, there often results, not a fusion of the two into a blended odor, as occurs with tastes, colors, and tones, but the stronger will supplant the other completely, or there will be an oscillation between the two. With some odors, again, there appears to be a true compensation. Thus, if two different olfactory stimuli of unequal strength are applied simultaneously, one will usually overpower the other completely; but if the stronger scent be diminished while the weaker is strengthened, a point may be found where the two blend into a single mixed odor. In other cases, however, a point is found where there is no sensation, *i.e.* the odors are perfectly compensated. An increase of either stimulus results in the sensation appropriate to it and there is no mixture whatever. The olfactory organ is easily fatigued, more so by some odors than by others, and it is found that when completely fatigued for one odor it may be insensible to some other odors, partially so to another group and wholly unaffected in its sensibility with reference to still another group.

Such experiments suggest points of departure for the study of olfactory qualities, and enough progress has already been made to suggest that the modal*i*ties of smell can be grouped into several graded series. The number of such groups will quite certainly be greater than those known for taste, where we have simply the four primary qualities, sweet, sour, salty, and bitter. Zwaardemaker's nine smell classes are as follows:

(1) Ethereal scents: Fruit odors.

(2) Aromatic scents: Camphor and spicy smells, anise, lavender, etc.

(3) Balsamic scents: Flower odors, vanilla, gum benzoin, etc.

(4) Ambrosiac scents: Amber, musk.

(5) Alliaceous scents: Garlic, ichthyol, vulcanized rubber, asafetida, bromine, chlorine, etc.

(6) Empyreumatic scents: Toast, tobacco smoke, naphtha, etc.

(7) Valeric, or hircine scents: Cheese, sweat, etc.

(8) Narcotic, or virulent scents: Opium, cimicine, etc.

(9) Nauseous scents, or stenches: Decaying animal matter, feces, etc.

The ability to discriminate different intensities of odors is not highly developed; in general, the least observable difference between two smell intensities of the same substance amounts to about one-third of the original stimulus. On the other hand, the olfactory organ is sensitive to exceedingly small amounts of the irritating substance, or as Ladd states it: "The sense has a great degree of 'sharpness,' or power to be excited by small quantities of stimulus, as distinguished from 'fineness,' or power to distinguish minute variations in the sensations." There are many familiar illustrations of this "sharpness." It is stated, for example, that in a liter of air 0.000005 gram of musk can be perceived, 0.000001 gram of sulphureted hydrogen and 0.000000005 gram of oil of peppermint. The sense is more delicate if the air containing the odorous substance is warmed.

Smell and taste are both chemically excited senses, but the olfactory organs can be excited by much more dilute solutions of the stimulating substances than can the gustatory organs. In the case of ethyl alcohol, which excites both of these receptors, the experiments of Parker and Stabler have shown that the organs of smell are sensitive to a dilution 24,000 times greater that that necessary to stimulate the organs of taste.

It is learned by suitable tests that the sensibility of the organ of smell is much more acute than the perception of odors. It was found in one series of tests, for example, that upon the average nine parts of camphor dissolved in 100,000 parts of water could be sensed by the nose, but without the perception of a definite odor, it requiring a solution of more than four times this strength before the specific odor could be recognized. Experiments made to determine the relative sensitiveness of men and women in this respect have thus far yielded conflicting results. With children it has been found that the sensibility (in the sense used above) increases up to the age of six years and then progressively diminishes. The delicacy of perception, on the other hand, measured by graded solutions of camphor, increases progressively with advancing age.

One source of perplexity in the classification of odors is the fact that some substances which have powerful odors in a state of great dilution are less effective in a state of high concentration. For some perfumes there appears to be an optimum vapor density below or above which the excitation is less strong. It has also been suggested that for unknown phylogenetic reasons some odors may have greater affective values than others, or it may be that fatigue of the sense of smell is *cæteribus paribus* less for those odors which have an element of utility to the species.

It must not be forgotten that some odorous substances affect the terminals of the trigeminus nerve in the respiratory part of the nasal passages, giving rise to tactile or other general sensation which may be combined with the olfactory sensations. This can be proven by plugging the olfactory sinus, when the trigeminal stimulus alone is perceived. Classification is further impeded by the universal confusion of tastes and odors. We say a substance "smells sweet," when as a matter of fact experiment shows that the modality sweetness can be perceived only by the sense of taste; and conversely most of the tastes of common experience are greatly affected by odors simultaneously sensed.

In the majority of persons (Toulouse and Vaschide) the left side of the nose is more sensitive than the right. With most of the other senses, on the other hand, there is an asymmetry in one-fifth of the cases in favor of the right side (van Biervliet). The difference is explained by the fact that the left side of the brain is more highly developed (in right-handed persons) and that the central olfactory tract does not cross before reaching its cortical centers, while those for the other senses do cross.

The measurement of olfactory sensations cannot easily be done absolutely in terms of the strength of the stimulus, though examples of the results of some attempts at the measurement of the threshold for smell in absolute terms are given above. To arrive at a relative measurement of olfactory values there are two methods chiefly in use. According to the method of Passy a number of flasks of equal size are provided and into each is put a measured quantity of the odorous substance, the quantities being arranged in a graded series. The substance may be allowed merely to diffuse itself through the air within the flask (which must be kept stoppered when not in use), or it may be dissolved in water or some other inodorous medium. By the use of a sufficiently extensive series, threshold values of different odorous substances may be determined and various other researches carried out.

The method of Passy is very laborious and for most purposes, particularly in clinical work, the olfactometer of Zwaardemaker is more convenient. In its simplest form it consists of a glass tube, curved at one end for insertion in the nostril and bearing a scale (preferably in centimeters), which slides with easy friction into a slightly larger tube which is lined with the odorous substance to be tested. The inner tube passes through a screen near its curved end. Now, when the outer tube is slipped completely over the inner tube so that its odorous lining is wholly covered by the latter, air drawn into the nostril through the inner tube will carry no odorous particles. If, however, the outer tube is slowly slipped off from the inner tube, the air current will pass over more and more of the exposed surface of the odorous substance before entering the inner tube, until a point will be reached at which the substance is just perceivable to the sense of smell. In this way the normal threshold can be determined for various substances and numerous tests of physiological and pathological interest carried out.

This simple apparatus has been modified in various ways. A very simple instrument which has the advantage of relative permanence of adjustment can be constructed by using a section of ordinary red rubber tubing for the outer tube. This should be slipped inside of a larger glass tube to prevent the odor from escaping from the outer side of the rubber, and the odor given off from the inner surface of the rubber tubing will remain quite constant for many months. For other odors the outer cylinder may be made of porous earthenware, whose pores may be filled with a solution of the odorous substance. Commonly the olfactometer is made double with a separate cylinder and breathing tube for each nostril, and for the study of the compensation of odors Zwaardemaker has constructed a very elaborate apparatus with two separate cylinders (one for each of the odors to be employed) connected with a single breathing tube and so adjusted that the amount of odorous surface exposed in each tube may be easily varied during the experiment. With the varying adjustments one odor or the other appears in consciousness alone until the proper compensation point is reached, when both odors vanish. The apparatus is provided with self-registering apparatus for recording on the kymograph the force of respiration in each cylinder and other data of the experiment.

The unit in all of these experiments is the "olfactie," or the stimulus necessary to produce the least perceivable sensation. The position on the scale of the olfactometer having been determined for this minimal value, this value is taken as the unit, or olfactie, and other stimuli are measured in multiples of this.

C. JUDSON HERRICK.

LITERATURE.

Bancels, J. L.: des. L'odorat. Revue générale et critique. Arch. de Psychol., t. x., pp. 1–46, 1910.

Bawden, H. H.: A Bibliography of the Literature on the Organ and Sense of Smell. Jour. Comp. Neur., vol. xi., No. 1, 1901.

Brookover, C.: The Olfactory Nerve, the Nervus Terminalis and the Preoptic Sympathetic System in Amia calva, L. Jour. Comp. Neur., vol. xx., No. 2, 1910; The Nervus Terminalis in Adult Man. Jour. Comp. Neur., vol. xxiv., 1914, p. 131.

Dieulafé, L.: Morphology and Embryology of the Nasal Fossæ of Vertebrates (Trans. by Loeb). Annals of Otology, Rhinol. and Laryngol., 1906.

Herrick, C. Judson: On the Phylogenetic Differentiation of the Organs of Smell and Taste. Jour. Comp. Neur., vol. xviii., 1908; The Nervus Terminalis (Nerve of Pinkus) in the Frog. Jour. Comp. Neur., vol. xix., 1909.

Jagodowski, K. P.: Zur Frage nach der Endigung des Geruchsnerven bei den Knochenfischen. Anat. Anz., Bd. xix., pp. 257–261, 1901.

Johnston J. B.: Nervus Terminalis in Reptiles and Mammals. Jour. Comp. Neur., vol. xxiii., pp. 97–120, 1913.

Landacre ,F. L.: The Origin of the Cranial Ganglia in Ameiurus. Jour. Comp. Neur., vol. xx., pp. 309–412, 1910.

Locy, W. A.: On a Newly Recognized Nerve Connected with the Fore-brain of Selachians. Anat. Anz., Bd. xxvi., Nos. 2–5, 1905.

McCotter, Rollo E.: The Connection of the Vomeronasal Nerves with the Accessory Olfactory Bulb in the Opossum and Other Mammals. Anat. Rec., vol. vi., pp. 299–318, 1912; The Nervus Terminalis in the Adult Dog and Cat. Jour. Comp. Neur., vol. xxiii., pp. 145–152, 1913; The Distribution of Nervus Terminalis in Man. Anat. Rec., vol. ix., 1915, p. 107.

McKibben, Paul S.: The Nervus Terminalis in Urodele Amphibia. Jour. Comp. Neur., vol. xxi., No. 3, 1911.

Nagel, W. A.: Vergleichende physiologische und anatomische Untersuchungen über den Geruchs- und Geschmackssinn und ihre Organe, mit einleitenden Betrachtungungen aus der allgemeinen vergleichendenden Sinnesphysiologie. Bibliotheca Zoologica, Heft 18, 208 pp., 7 plates and a bibliography of 335 titles. Stuttgart, 1894.

Parker, G. H.: The Relation of Smell, Taste, and the Common Chemical Sense in Vertebrates. Jour. Acad. Nat. Sci. Philad., vol. xv., 2 Ser., pp. 221–234, 1912.

Parker, G. H. and Stabler, E. M.: On Certain Distinctions between Taste and Smell. Am. Jour. Physiol., vol. xxxii., No. 4, 1913.

Passy: Revues générales sur les sensations olfactives. L'Année Psychol., vol. ii., 1896.

Pinkus, F.: Ueber einen noch nicht beschreibenen Hirnnerven des Protopterus annectens. Anat. Anz., Bd. ix., pp. 562–566, 1894.

Read, Effie A.: A Contribution to the Knowledge of the Olfactory Apparatus in Dog, Cat, and Man. Am. Jour. Anat., vol. viii., No. 1, 1908.

Sheldon, R. E.: The Reactions of the Dogfish to Chemical Stimuli. Jour. Comp. Neur., vol. xix., pp. 273–312, 1909; The Sense of Smell in Selachians. Jour. Exp. Zool., vol. x., No. 1, 1911.

Zuckerkandl, E.: Ueber das Riechcentrum. Stuttgart, 1887; Normale und pathologische Anatomie der Nasenhöhle und ihre pneumatischen Anhänge. 2 Ed., Wien and Leipzig, 1893; Das Jacobsonsche Organ. Merkel und Bonnet's Ergebnisse, Bd. xviii., pp. 801–843, 1910.

Zwaardemaker, H. Die Physiologie des Geruchs. Leipzig, Engelmann, 1895; Les sensations olfactives, leurs combinaisons et leurs compensations, Année psychol., vol. v., 1899; Revue générale sur l'olfaction, Année psychol., vol. vi., 1900; Geruch. Ergebnisse der Physiol., Bd. 1 (II), 1902.

Olibanum.—*Frankincense. Thus. Gummi-resina olibani.*—A gum resin obtained from *Boswellia carterii* Birdw. and other species of *Boswellia* (fam. *Burseraceæ*).

Olibanum is collected in northeastern Africa, chiefly by the Somali natives, and is mostly exported viâ India. It is produced by small trees similar to those which yield myrrh, and is chiefly obtained from incisions made for the purpose. It exudes as a thick milky juice, hardening into the tears described below, which preserve their white color much longer than those of other similar substances.

Olibanum occurs in irregularly oval or subglobular tears, separate, or occasionally somewhat agglutinated in the poorer grades, usually 1.25 centimeters (0.5 inch) or less in diameter, from almost pure white to yellowish-white, occasionally reddish-brown when long kept, the surface powdery; breaking readily with a nearly flat, waxy, lustrous surface, translucent in thin fragments; odor balsamic, slightly like turpentine; softening between the teeth, aromatic and somewhat bitter. Triturated with water, it forms a white emulsion and is almost wholly soluble in alcohol. When burned, it emits a very strong and pleasant odor, on account of which it is used as incense.

Olibanum consists principally of resin, usually from 60 to 70 per cent., or occasionally 75 per cent., with from 30 to 35 per cent. of gum and from 3 to 8 per cent. of volatile oil. Its bitter principle has not been examined. The volatile oil, which is an article of commerce for perfuming purposes, combines a slight lemon-like odor with that of the drug, and is of complex composition. The resin is divisible into two portions, namely, *Boswellic* or *Boswellinic acid* and *olibano-resin*. The gum is more like acacia than like tragacanth.

From a medicinal point of view, the uses of olibanum are quite unimportant. It is no longer official in any leading pharmacopœia and is but little used in professional medicine.

Owing to its fragrant properties, it is with some a favorite ingredient of plasters and ointments, and it is elsewhere used for odorizing purposes. It has mild counterirritant and disinfectant properties, leading to its use as a vulnerary. Internally, it possesses the ordinary stimulating diuretic and expectorant properties of the oleoresins, and it also has a considerable use, especially among the laity, based chiefly on religious fancy, as an emmenagogue. The dose is from gr. xv.–xlv. (1.0–3.0). It is used chiefly, perhaps, in the form of the emulsion, although the tincture is to be preferred.

Henry H. Rusby.

Oligemia.—A decrease in the total mass of the blood. The term is often used incorrectly as a synonym for anemia. The latter term is used to indicate a deficient supply of blood to a part, or a deficiency in the total amount of blood within the body, or, most commonly, to designate a decrease in the number of the red cells or a diminution of the hemoglobin. The expression *general anemia* may, therefore, be regarded as expressing the same idea as that conveyed in oligemia. The decrease in the total mass of blood may be due to a number of causes, and the following varieties may be distinguished:

Oligemia Vera.—True oligemia is due to a sudden loss of blood through hemorrhage. A loss of half of the total mass of the blood is invariably fatal, and hemorrhages of even less degree may cause death. The red cells may drop after a single large hemorrhage as low as 2,000,000. After such a loss of blood there is a rapid fall in blood pressure, the heart is incompletely filled, the pulse becoming very small, frequent, and irregular. Cardiac activity is at first increased, then lowered after a time. The blood-vessels become contracted at first in the effort to keep up the blood pressure; but after a time the larger vessels dilate, the smaller ones alone remaining contracted. The threatening symptoms in oligemia are small and rapid pulse, nausea, vomiting, feeling of anxiety, syncope, convulsions, and coma. The loss of one-half kilogram can produce syncope, while hemorrhages of one and one-half to two kilograms are usually fatal. Even smaller losses may cause death. Treatment consists of infusions of physiological salt solutions. In cases of hemorrhage of slight degree, but continued through a long period of time, the deficiency is partly made up by an increase in the fluids of the blood, the true oligemia becoming thus converted into a hydremic oligemia. Oligemia vera occurs also in many cachectic conditions (carcinoma, tuberculosis, pernicious anemia, chronic suppurations, etc.). In pernicious anemia the cadaver in extreme cases may seem to be almost wholly devoid of blood.

Oligemia Hydremica or Serosa.—An oligemia with increase of water in the blood, the red cells and albumin being diminished, occurs after all hemorrhages, particularly in the case of oft-repeated or prolonged hemorrhages of slight degree, as in bleeding piles, excessive menstruation, etc., also in conditions characterized by loss of albumin, as in chronic nephritis, dysentery, chronic suppurations, prolonged lactation, tumor cachexias, scurvy, malaria, etc. The hydremic condition of the blood leads to pathological changes in the blood-vessel walls, favoring the passage of fluids and the increased production of lymph (edema). Hydremia is, however, not the direct factor in the production of edema, but only a favoring one.

Oligemia Sicca (*Inspissatio Sanguinis, Anhydremia*).—A thickening of the blood through loss of water may lead to a decrease of the total mass. Such a condition may occur in cholera, dysentery, severe diarrheas, excessive sweating, insufficient supply of water, etc. The highest degree of oligemia sicca occurs in Asiatic cholera. As a result of the circulatory disturbances thus produced, and an insufficient supply of blood to the nervous centers, the characteristic symptoms of severe anemia may arise, although the total number of red cells and total amount of salts and albumin in the blood are not decreased. The thickened blood is dark and tarry; the number of red cells is increased to 6,000,000 to 8,000,000 per cubic millimeter. As the result of the increased viscosity the circulation is impeded and the work of the heart increased. The blood serum is richer in albumin and in salts. The body tissues become very dry, and non-encapsulated serous exudates are resorbed.

Oligemia Oligocythemica.—A decrease in the total blood mass due to a diminution in the number of red cells (see *Oligocythemia*).

brush-discharge, give greater relief than wet dressings or other external applications.

In *early local neuritis* before the establishment of a marked degree of exudation and infiltration it may be possible to relieve the condition with radiant light and heat, though in no case of any length of duration can it cure the condition, though relieving the local pain which effect is but temporary in character.

One other valuable use of radiant light and heat is in the treatment of *x-ray dermatitis*, that is, in the cases that arise in the course of treatment. When employed with sufficient energy prior to the ulcerative stage of an *x*-ray dermatitis, ulceration may in all cases be prevented. It requires prolonged applications, however, to offset the serious forms of *x*-ray dermatitis. After the ulcerative stage it is of comparatively little value at first as the slough must be removed before any active restitution can take place; that accomplished, however, there is probably no agent more effective in bringing about restitution than radiant light and heat.

The treatment of coryzas, colds in the head, or even chronic nasal catarrh, or laryngitis by prolonged use of radiant light and heat applied to the extent of toleration, that is, as hot as can be tolerated with the lamp suspended over the patient reclining, is remarkably effective. It will rarely require more than two such applications with a 50 c.p. therapeutic lamp to abort entirely an acute coryza.

In *acute laryngitis* the additional use of the static wave current will add greatly to the promptness of cure of the condition.

The incandescent light bath in conditions of *hypertension* and general depression of metabolism is one of the most useful means that can be employed, and properly belongs in the home of aged people and of those who wish to preserve their vigor and youthfulness. Light baths, taken daily or every alternate day, after the day's fatigue is refreshing and delightful. This followed by a shower, before retiring will insure in most cases a quiet slumber. By reducing the amount of fluid by perspiration and by relaxation of the peripheral arteries it affords great temporary relief in conditions of hypertension.

There are many other similar conditions which may be treated successfully with radiant light and heat. The foregoing, however, outlines the general principles, and the classes of cases in which they are indicated.

WILLIAM BENHAM SNOW.

Phrenic Nerve.—ANATOMY.—The phrenic nerve, or the internal respiratory nerve of Bell, is the principal motor nerve of the diaphragm. It originates in the ventral gray column of the spinal cord from the middle of the third to the sixth cervical segments. Its fibers leave the cord mainly in the fourth cervical roots, with usually some additions from the third or fifth root or both of these. Schroeder and Green give its origins as follows:

	Number of cases.	Fourth only.	Fourth and fifth.	Third, fourth, and fifth.	Third and fourth.
Luschka........	32	12	7	7	6
Brook..........	16	4	9	3	0
Green..........	52	9	21	13	9
Total........	100	25–25 %	37–37 %	23–23 %	15–15 %

When there is a single root, it is always from the fourth nerve.

The course of the nerve is somewhat different on the two sides. It passes downward in the neck over the scalenus anterior muscle; then diagonally downward and outward, it passes in front of the first part of the subclavian artery and behind the subclavian vein. In about four per cent. of cases, however, the nerve passes in front of the vein, and so lies immediately behind the clavicle. Two cases are on record in which the nerve passed through the vein. Passing into the thorax it lies, on the right side, external to and slightly behind the right innominate vein and the superior vena cava; on the left side, in front of the arch of the aorta. On both sides it passes between the pleura and the pericardium, anteriorly to the roots of the lungs; on the right side being in close contact with the root, and on the left side passing out and to the left, in order to pass around the heart. The right nerve has an almost vertical direction, and passes to the upper surface of the diaphragm, where it divides into from three to six branches, which pierce the diaphragm externally to and in front of the opening for the inferior vena cava. The left nerve has a more circuitous route, and generally divides in the substance of the diaphragm.

Branches.—1. Communicating: (1) From the upper ganglion of the cervical sympathetic gangliated cord. (2) Occasionally, from the loop formed by the descendens and communicans hypoglossi. (3) From the nerve to the subclavius. (4) The right nerve, at its termination, sends branches to the right semilunar ganglion of the celiac plexus. (5) The left communicates with the sympathetic plexus to the esophagus above the diaphragm.

2. Distribution: (1) On the right side, to the superior vena cava. (2) Pleural branches, from one to three in number. (3) Branches to the pericardium, usually three. (4) Luschka has described twigs to the right auricle. (5) Terminal branches to the diaphragm. This is the main distribution of the nerve. It supplies the entire diaphragm except an area along the costal margin, about three centimeters in width, which is supplied by the lower six intercostal nerves, and an indeterminate area on the crura, probably supplied by the vagus.

The innervation of the diaphragm by the phrenic nerve from the cervical spinal cord at a level above that from which the intercostal muscles are innervated (thoracic cord) is explained by the evolutionary history of the diaphragm, viz., its origin from muscles lying in the cervical region in Amphibia.

The phrenic nerve contains large and small myelinated fibers and also unmyelinated fibers. The motor end-plates in the diaphragm resemble those of other voluntary muscles (Aoyagi). Sensory fibers are known to occur in the phrenic nerve (see the review by L. J. Kidd in the *Review of Neurology and Psychiatry*, vol. ix., 1911, p. 587), and referred pains in the shoulder are frequent in visceral disease affecting this nerve. Nevertheless the stimulation of the central end of the divided phrenic nerve within the thorax of the rabbit causes no reflex movements of any sort (Porter and Turner, *Am. Jour. Physiol.*, vol. xxxii., 1913).

PHYSIOLOGY.—The chief physiological function of the nerve is that of the principal motor nerve supply to the diaphragm.

PATHOLOGY.—1. Paralysis of half of the diaphragm, as a result of inflammation or degeneration of the phrenic nerve on the corresponding side, from exposure, lead poisoning, or compression, may occasionally occur. The condition generally comes on slowly and is characterized by inversion of the type of respiration, which reduces intraabdominal pressure, causing difficulty in defecation, etc. Respiration is usually affected only during exertion, when dyspnea results.

2. Neuralgia. Some authorities describe a form of neuralgia characterized by pain in the lower and anterior part of the thorax, along the line of diaphragmatic attachment, extending up into the neck and along the inside of the arm, with painful areas at the points where the nerve becomes superficial. This

condition is said to complicate angina pectoris, Graves' disease, and some forms of cardiac disease.

3. Surgical Pathology. Injury to or division of the nerve may occur in gunshot wounds or stab wounds, or in the course of surgical operations. This complication has generally been regarded as fatal, and the statement has been generally made in the surgical literature that it is necessarily so. Schroeder and Green after a review of the literature show that there are only six cases on record in which the nerve was injured. In all other cases, usually reported as injuries of the phrenic nerve, an examination of the original article shows that some other adjacent structure had been injured instead of the phrenic. Of the six cases of actual injury to the nerve, in the first four (those reported by Schurmayer, Beck, Bardeleben, and Erichsen) there was also injury to some other important structure, which was alone sufficient to cause death. Of the two cases of injury to the nerve alone, the first (reported by Mackenzie) was instantly fatal. The second (reported by Schroeder in 1902) ended in recovery, with paralysis of the corresponding half of the diaphragm. Mackenzie's case was that of an Indian coolie, who suddenly fell dead, and on postmorten examination the reporter was unable to find any sufficient cause of death, except a rupture of the right phrenic nerve. It hardly follows, however, that the rupture of the nerve was the cause of death.

Schroeder's case, then, is the only one on record in which the phrenic was injured without injury to surrounding structures, and in which the exact extent of the injury was known. Schroeder and Green report the following experimental researches and summary:

1. On the Human Being. In eighteen cases of tuberculous glands of the neck, the nerve was pinched during operation with the following results: Contraction of the corresponding half of the diaphragm, with sudden rising of the anterior abdominal surface below the costal arch. In ten cases the right nerve was pinched and the left in eight. In one case on each side there was some pain in the region of the diaphragm, but it subsided in forty-eight hours. The symptoms usually attributed to irritation of the diaphragm (*i.e.* sneezing, coughing, and hiccoughing) were not observed in a single instance.

2. On Dogs. In the course of an extended series of experiments on dogs, the following results were obtained: After resecting as much as possible of the cervical portion of the nerve, it was found that after resection of one nerve only, there was an increased thoracic expansion and a slight abdominal retraction, changes which were more evident on the divided side than on the normal side. In case of a double resection there occurred an inverted type of respiration, *i.e.* decided retraction on inspiration and increased thoracic expansion, due to the action of the accessory respiratory muscles. In unilateral resection kymographic tracings showed that the normal half of the diaphragm rose half an inch on inspiration and fell the same distance on expiration, while the half of the diaphragm on the side on which the nerve had been resected moved only an eighth of an inch, as it was moved passively by the movements of the normal side. After division of the nerve, the diaphragm becomes relaxed and the muscle arches up into the thorax. The type of respiration becomes increasingly costal when one nerve is divided, and inverted when both nerves are cut. The accessory respiratory muscles become very active. There is no sneezing or coughing. In one case of double division the respiration became labored, but remained so for only a few days.

Postmortem Findings.—In cases in which the dogs were killed in from seven to fourteen days after resection of the nerve, the atrophy of the diaphragm was not great and the color was reddish yellow. When a longer time had elapsed, the atrophy was marked, the paralyzed part being thin and flabby, the color pale yellow, and in older cases translucent. In all cases there remained a margin from one-quarter to three-eighths of an inch in width at the costal border, which retained its normal color and thickness. This margin is supplied by the intercostal nerves.

SUMMARY.—1. From clinical, experimental, and anatomical data it would seem that the diaphragm is not an essential muscle of respiration, and that the importance of injury to its principal nerve, the phrenic, has been exaggerated. Injury to the phrenic or division of one nerve is not necessarily fatal. It may, however, predispose to lung infection or be followed by diaphragmatic hernia.

2. While the diaphragm is supplied with branches from the lower six intercostal nerves, they are inferior to the phrenic in importance and unable to take the place of the phrenic after division of the latter.

A bibliography of fifty-nine titles is given in the article from which the preceding summary is taken (W. E. Schroeder and F. R. Green, Phrenic Nerve Injuries, *Am. Jour. of the Medical Sciences*, N. S., vol. cxxiii., p. 196, 1902). C. JUDSON HERRICK.

Phrenosin is a cerebrin present in the nervous tissues which is probably identical with cerebron. See *Cerebrosides.* F. P. U.

Phthirius.—A genus of lice which contains *P. pubis* (*P. inguinalis*), the crab-louse. This insect usually infests the hairs of the pubic region, but may be found in the arm pits, or even in the beard, moustache, eyelids, or scalp. It is usually eliminated without difficulty by the use of mercurial ointment. See *Insects, parasitic.* A. S. P.

Physaloptera.—A genus of roundworms. Two species have each been reported once as parasites of man: *P. caucasia* in the Caucasus, *P. mordens* in Unganda. See *Nematoda.* A. S.P.

Physick, Philip Syng.—Born in Philadelphia, Pa., July 7, 1768. His early medical studies were prosecuted in his native city, but in 1789 he went to England and placed himself under the instruction of John Hunter, in London. Living, as he did, in the home of this great physiologist and surgeon, and being of an observant type of mind, he rapidly absorbed the best anatomical and surgical knowledge that was obtainable in London at that time. In 1790 he was given the post of House-Surgeon at St. George's Hospital, and remained on duty at that institution for one year. In May, 1792, he received the degree of Doctor of Medicine from the University of Edinburgh, and in September of the same year he returned to Philadelphia, and began the practice of his profession. In 1794 he was elected one of the attending surgeons of the Pennsylvania Hospital, and in 1805 he was given the independent Chair of Surgery in the University of Pennsylvania. This was the first separate Professorship of Surgery established in America, and Dr. Physick held the position during the following thirteen years. His success as a teacher of surgery was great, and justified fully the appellation of "Father of American Surgery" which was afterward bestowed upon him.

One of the most important contributions made by Dr. Physick (about the year 1800) to surgical therapeutics was his method of treating hip-joint disease. He died at his home in Philadelphia on Dec. 15, 1837. During a large part of his life he had been a frequent, almost a constant, sufferer from a variety of bodily ills. A. H. B.

subarachnoid space, myelomeningocele; and in the central canal of the cord, syringomyelocele. Von Recklinghausen added a fourth or a mixed form—fluid distending both the central canal and the subarachnoid space; this is rare.

A fifth type is the anterior spina bifida; also a rare condition where the bodies of vertebræ are cleft instead of the arches; sometimes both the bodies and the arches are cleft—spina bifida anterior and posterior (Fig. 4552).

A sixth type is spina bifida occulta, where a spina bifida sac was present in the fetus, but disappeared before birth.

These six types behave differently; some are amenable to surgical treatment; others are not; we should differentiate between them in diagnosis.

Myelomeningocele.—To this type (according to Sharpe, *Annals of Surgery*, 1915, pp. 151–165) belong seventy to eighty per cent. The subarachnoid space is filled with sac fluid anterior to the cord or the cauda equina which is crowded backward out of the spinal canal, and usually adheres to the top of the sac, at which point the dura mater is absent. What may be another form of fluid in the subarachnoid space, and may therefore be regarded as a form of myelomeningocele, is pictured in Fig. 4553. Here fluid is collected in the reticulum of the arachnoid posterior to the spinal cord: it forms a sac full of cyst-like cavities; the spinal cord or cauda equina are not in the sac, though occasionally a loop of nerve root may be found in it.

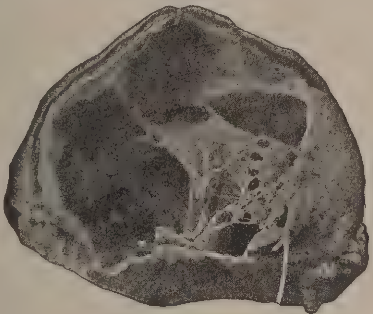

Fig. 4553.—Myelomeningocele; Sac much Subdivided. (Warren Museum.)

In the classical form of myelomeningocele, the spinal cord adheres to the apex of the sac wall where it loses its form, flattens and bcomes a part of the wall of the sac, so that looking within the opened sac (Fig. 4554) the nerve roots rise in a double row from the sac wall, and cross the cavity to the intervertebral foramina.

Myelomeningoceles occur in the lower half of the spine; they are very rare in the cervical region. It is typical of myelomeningoceles that the cleft arches extend through four, five, six, or seven adjacent vertebræ; that the arches are wide open from side to side; that the sac has a broad base, is irregularly ovoid and seldom projects upon the surface of the back as much as its length.

Skin covers the base of the protrusion merging into semi-transparent membrane and becoming thin and cyanotic as it approaches the membrane, which often covers half or two-thirds of the surface. Upon this membrane may be found granulating ulcers; clear, watery fluid, like cerebrospinal fluid, may exude in drops or escape through small perforations. The membrane is sometimes dense and tough, resembling old scars; often it is as thin and friable as tissue paper. Often the center is depressed giving the tumor the shape of a tomato, the umbilication indicating the point at which the spinal cord is attached. A surgical incision through the umbilication is to be shunned. The skin on the back near the base is normal, but hairy.

Where the cord is attached to the sac it is malformed and flattens out. Where fluid collects in the meshes of the arachnoid back of the cord, it crowds the cord from behind against the vertebral bodies, so that softening may take place. The lengthened nerve roots are swollen, purple from venous stasis, and often devoid of axis cylinders. These nerve lesions are permanent changes cutting off the nerve supply.

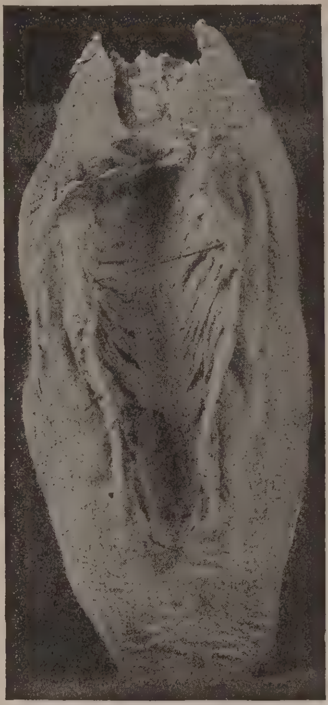

Fig. 4554.—Section through a Myelomeningocele. The lumbar enlargement is attached to the posterior wall of the sac, and has been divided. The nerve roots are seen running from this part of the posterior sac wall toward the foramina. (Warren Museum.)

The resulting motor paralysis in the legs is usually distributed symmetrically; sensory disturbances, like areas of anesthesia, may also be found and sphincter paralysis expressed by rectal or vesical incontinence—or both; trophic ulcers of the feet and legs are not uncommon; paralytic club-feet, congenital dislocation of the hip, hydrocephalus, and other malformations are common.

The span of life of untreated babies with myelomeningocele is short; nine out of ten die in their first year, mostly within two months of birth. Surgical intervention, to-day the usual treatment, decreases mortality from ninety to fifty per cent.; it aims to empty excessive fluid by incision, to replace the spinal cord and nerve roots within the spinal canal and to cover it with healthy skin, eliminating the danger of rupture of the sac and of fatal septic meningitis. Paralysis is seldom benefited by operation, and closing the sac may increase hydrocephalus or may cause it to appear. Spontaneous cure from ulceration, cicatricing, and shrinkage of the sac occasionally occurs.

Hydromeningocele, or simple spinal meningocele, represents the next commonest form occurring in eight to twelve per cent. (according to Sharpe, *loc. cit.*). The fluid is in the subdural space, the cavity is without cord or nerves. The external form is globular, from the size of a grape to that of the child's head, and large ones may burst during birth. The base is small, the cleft arches are not spread open widely, and only one, two or, at most, three adjacent vertebræ are split. Rare cases are on record of the sac escaping through a hole in the ligamentum subflavum the spinous process being partly bifid. Normal skin covers the sac entirely or leaves only a small area of membrane. By transillumination, used as for hydrocele of the tunica vaginalis, the light is easily transmitted and there are no shadows or dark bands which one may see in myelomeningoceles from nerve roots and cross partitions.

Hydromeningocele frequents the sacral and lumbosacral region, is decidedly uncommon in the lumbar and cervical spine, and very rare in the dorsal. Hydrocephalus may be present, but paralysis almost never. Rupture of the sac is not uncommon and may lead to death from shock or septic meningitis. Spontaneous cures from shrinking have been recorded.

Surgical intervention (dissection and ligation of the neck of the sac, and closing the wound) is safe and easy even after accidental rupture. Prognosis after recovery from operation is good except for that unknowable factor hydrocephalus.

Syringomyelocele.—This type is rare, less than one per cent., even, including the mixed form of von Recklinghausen. Sac fluid distends the central canal of the cord; consequently the distended cord forms the lining of the sac. The committee of the London Clinical Society found only two cases of syringomyelocele—one lumbar and one cervical. Von Recklinghausen reported eleven of the mixed forms. In the syringomyelocele only two arches were cleft; in Recklinghausen's mixed form, four, five, or six. The external covering is skin. The translucency tested is like that for hydromeningocele which it resembles in many ways.

Other malformations are as a rule present especially in von Recklinghausen's form and the prevalence of grave deformities like congenital hernia of the liver, or of liver and intestines, and exstrophy of the bladder is remarkable. Abnormal spinal curvatures, like congenital scoliosis are common, likewise thoracic malformations, the absent, bifid or bicipital ribs. Paralysis of legs and sphincters is common. The prognosis untreated is worse than for myelomeningocele; with operation the prognosis is also poor. A syringomyelocele may come to operation, supposing it erroneously to be a hydromeningocele; when recognized the graver prognosis should be given. A search through the literature has so far failed to establish the existence of an adult with syringomyelocele.

Anterior spina bifida. This form and the anterior and posterior form are rareties.

The body of a vertebra ossifies from two centers—a right and a left one and it is common to find vertebræ ossified on the sides but cartilaginous in the median vertical plane. The anterior spina bifida sac escapes from the canal through a hole in this cartilaginous part, and protrudes into the abdomen or pelvis. The anterior type is reported in girls almost exclusively, usually it is in the sacrum. The sac fluid is said to be in the subdural space; nevertheless, paralytic club-feet, and paraplegia have been observed. Large tumors have been mistaken for sarcoma or pelvic cysts. A specimen in the Warren Museum, Boston (Fig. 4552) represents an extensive anterior and posterior cleft of the upper half of the spine, and precluded further development. The prognosis for anterior spina bifida is bad; a few operated upon have died.

Spina Bifida Occulta.—This interesting condition is not rare; it may occur in five per cent. It is little studied, often overlooked or wrongly diagnosed. Radiograms of the spine taken for other reasons, not infrequently reveal its unexpected presence. The hypertrichosis, hair over the cleft, often does not develop until after puberty. There is no protruding sac; there may be an old scar, or wrinkled pigmented skin, or a median nevus, or simply the hair. The ends of the laminæ may be palpable, or they may be concealed by a diffuse growth of fat, a congenital lipoma. Angiomata or dermoid cysts, as well as lipomata, have been found there expanding both within and outside the spinal canal, connected by a slender stem like that of a shirt stud. Some have found that the skin or fascia adhered to nerve roots or cauda equina.

Paralysis, anesthetic areas, and trophic ulcers may be present and they may not appear till late childhood or adolescence. In little children and in infancy the condition may be overlooked entirely and symptomless adults with hypertrichosis are exhibited at circus side shows as the man or woman with a horse's mane.

This delayed appearance of involvement of the spinal cord and nerve roots has been attributed to the slowly increasing intraspinal pressure from tumor growths, or to a drag upon the spinal cord from its attachment to the faster growing spinal column; for at birth the cord ends at the third lumbar and in adults at the first lumbar vertebra.

The frequency of abnormal curvatures of the spinal column in connection with deficient spinal arches may explain the unexpected detection of spina bifida occulta among scoliotics when a radiogram of the spine became a routine measure for clinic patients.

Treatment has so far been limited to the attempts of some surgeons to relieve intraspinal pressure by removing the tumor. The published results are encouraging.

Spontaneous cure of spina bifida occulta paralysis has not been observed. Trophic ulcers may heal, but are apt to return.

Augustus Thorndike.

Spinal Cord and Spinal Nerves.

General Description.—The spinal cord (*Medulla spinalis*) is that portion of the central cerebrospinal nervous system which is situated within the vertebral canal (Figs. 4555 to 4558). The human spinal cord is a slightly flattened cylinder, varying in caliber somewhat at different levels. It is bent in the sagittal plane corresponding to the curvature of the vertebral column. It is from forty-three to forty-five centimeters in length, being on the average somewhat longer in the male than in the female. It is continuous above, at the lower edge of the foramen magnum, with the medulla oblongata, and extends below into the lumbar part of the vertebral canal, where it is abruptly drawn out into a terminal filament (*filum terminale*).

The spinal cord of the embryo fills the entire cavity of the vertebral canal, and this condition prevails throughout early fetal life (Fig. 4558). But in later development both the diameter and the length of the vertebral canal increase more rapidly than do those of the spinal cord. The result is that in the adult the spinal cord, exclusive of the terminal filament, usually ends at or near the level of the first lumbar vertebra. Nor does the spinal cord come anywhere near filling up the lumen of the vertebral canal. A cross-section through the vertebral canal with the cord *in situ* reveals a large space between the surface of the cord and the inner surface of the bony vertebral canal (Fig. 4556). This space is subdivided by the coverings of the cord into several spaces. One of these, between the arachnoid membrane and the pia mater, the so-called subarachnoid cavity (*cavum subarachnoidale*), is filled with the cerebrospinal fluid (*liquor cerebrospinalis*). This disproportion between the size of the cord and that of the cavity of the vertebral canal is of great significance for the protection of the cord from injury during the various movements which the vertebral column undergoes.

The regions of the spinal cord are named according to the nerve roots with which they are connected (see below). We have, accordingly, cervical, thoracic, and lumbar parts. Below the latter the cord diminishes rapidly in caliber, this part being called the medullary cone (*conus medullaris*). From the lower end of the medullary cone the terminal filament extends downward as a delicate strand for a distance of from twenty to twenty-five centimeters, to end upon the dorsal surface of the os coccygis (Fig. 4557).

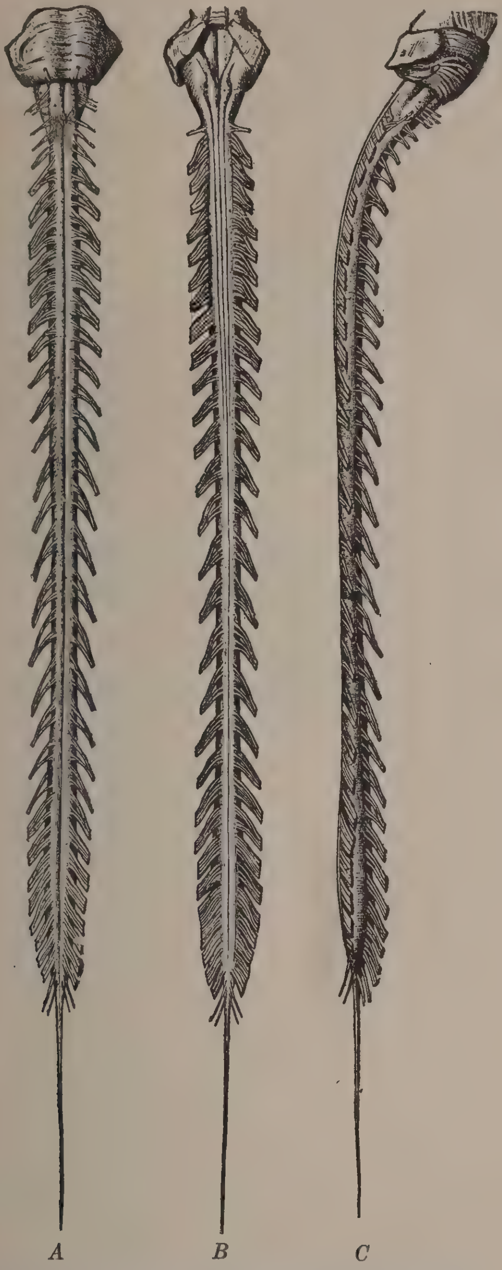

FIG. 4555.—Views of the Spinal Cord (Medulla Spinalis). *A*, From in front; *B*, from behind; *C*, from the right side. (From Toldt.)

The spinal cord, though in general of cylindrical shape, is everywhere flattened from before backward. It is considerably enlarged in two regions. The upper enlargement is situated at the junction of the neck and thorax, and is known as the cervical enlargement (*intumescentia cervicalis*); its maximal size is opposite the fifth or sixth cervical vertebra, where the sagittal diameter is 9 millimeters and the transverse diameter 13 to 14 millimeters. The lower enlargement, at the junction of the thoracic with the lumbar portion of the spinal column, is known as the lumbar enlargement (*intumescentia lumbalis*); the maximum of this enlargement is reached at the level of the twelfth thoracic vertebra, where the sagittal diameter is about 8.5 millimeters and the transverse diameter 11 to 13 millimeters. These two enlargements correspond to the places where the spinal cord gives off nerves to, and receives nerves from, the upper and lower extremities respectively.

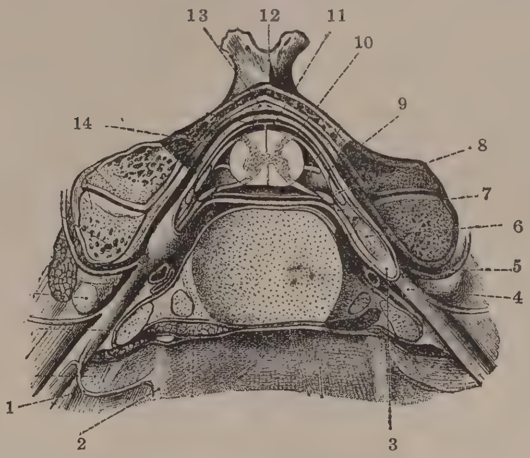

FIG. 4556.—Transverse Section through the Intervertebral Fibrocartilage between the Third and Fourth Cervical Vertebræ. The spinal meninges are shown in cross-section and their relations to the spinal nerves are indicated. (After C. Toldt, "Anatomischer Atlas," Wien, 1900.) 1, Ramus communicans; 2, trunk of the sympathetic; 3, fourth spinal nerve; 4, ramus ventralis; 5, ramus dorsalis; 6, ganglion spinale; 7, radix ventralis; 8, radix dorsalis; 9, spinal dura mater; 10, subarachnoid space; 11, spinal arachnoid; 12, spinous process of the third cervical vertebra; 13, subdural space; 14, epidural space.

Upper and Lower Limits of Cord.—The upper limit of the spinal cord in man and mammals corresponds to the lateral exit of the uppermost rootlets of the first cervical nerve. This point corresponds ventralward to the lowermost bundles of the decussation of the pyramids. The lower level of the cord, that is its junction with the filum terminale, nearly always lies on a level corresponding to the lower third of the first lumbar vertebra or the upper third of the second lumbar vertebra, though in forty per cent. of the cases it may lie opposite the upper two-thirds of the first lumbar or the lower two-thirds of the second lumbar vertebra. In one case it ended five milli-

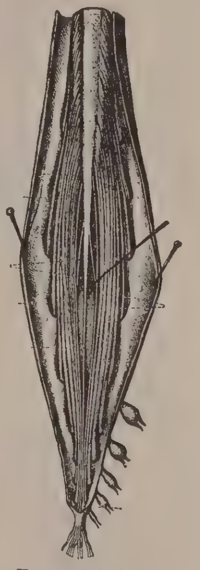

FIG. 4557.—The Lumbar Spinal Cord (pars lumbalis medullæ spinalis) with the terminal cone (conus medullaris), terminal thread (filum terminale), and the horse's tail (cauda equina), Viewed from behind. (After C. Toldt, "Anatomischer Atlas." Wien, 1900.)

meters above the lower border of the twelfth thoracic vertebra, and it has been found as far down as the lower margin of the second lumbar vertebra. (See report of Committee of Collective Investigation of Anatomical Society of Great Britain and Ireland for the year 1893–94, *Jour. Anat. and Physiol.*, vol. xxix., 1895, pp. 35–60.)

Length of Spinal Cord.—The extreme variations in the male are between 44 and 50.6 centimeters; in the female, between 39 and 47 centimeters. As to the relation of the length of the cord and the length of the vertebral column, measured from the foramen magnum to the basis ossis sacri, it may be stated that when the average length of the spinal column is designated 100, the length of the male spinal cord will be 64, that of the female spinal cord about the same. The average length of the vertebral column in the male is 70 centimeters; in the female, 68 centimeters (Ziehen).

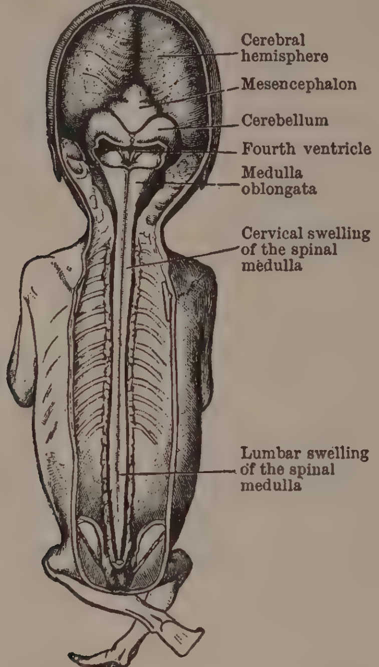
Cerebral hemisphere
Mesencephalon
Cerebellum
Fourth ventricle
Medulla oblongata
Cervical swelling of the spinal medulla
Lumbar swelling of the spinal medulla

Fig. 4558.—Human Fetus in the Third Month of Development, with the Brain and Spinal Cord Exposed from Behind. (Cunningham.)

Upper Level of Conus Medullaris.—Charpy designates as the arbitrary upper limit of the conus medullaris a plane lying between the exit of the fifth sacral nerve and the nervus coccygeus. According to this the conus medullaris would measure about ten millimeters in length. Raymond states that clinicians usually regard the conus medullaris as extending farther up, usually to the plane between the third and fourth sacral nerve roots. This would make the conus medullaris considerably longer.

Segments of the Spinal Cord.—The nerve fibers which compose the spinal nerves are arranged in small fascicles or radicular threads (*fila radicularia*) which connect with the spinal cord in two rows on each side. These are the dorsal or posterior and the ventral or anterior root fibers. The dorsal and ventral rows of radicular threads as they pass out lateralward to leave the vertebral canal converge toward their respective intervertebral foramina, thus constituting the trunks of the spinal nerves. Each nerve trunk is described as composed of two roots, a dorsal root (*radix dorsalis*), comprising the radicular threads which enter it from the dorsal side of the cord, and a ventral root (*radix ventralis*), comprising the radicular threads from the ventral side of the cord. On each dorsal root just before its union with a ventral root is a small swelling containing the cell bodies of the neurones of the dorsal root fibers. This is the spinal ganglion (*ganglion spinale*). The spinal cord is divided into a series of longitudinally arranged segments, each of which is connected by means of its dorsal and ventral fila radicularia with a pair of spinal nerve trunks. The segments are named in accordance with the related spinal nerves, and the latter are named after the vertebræ contiguous to their foramina.

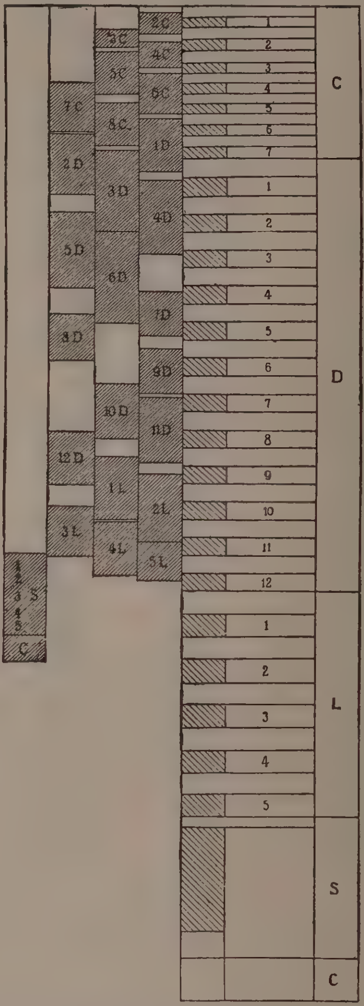

Fig. 4559.—Topographical Relations between the Spinous Processes of the Vertebræ and the Roots of the Spinal Nerves. The letters *C*, *D*, *L*, *S*, *C*, in the unshaded rectangular spaces to the right indicate the longitudinal extent of the cervical, thoracic, lumbar, sacral, and coccygeal portions of the spinal column. The rectangular spaces shaded obliquely from the left and above downward and to the right indicate the longitudinal extent of the spinous processes of the individual vertebræ, while the rectangular spaces shaded obliquely from the right and above downward and to the left, indicate the region within which the origin of the individual roots of the spinal nerves is to be sought. The horizontal extent of the rectangular space has no significance. (After Reid, *Journ. Anat. and Physiol.*, Lond., 1889, p. 341.)

Relation of Individual Spinal-cord Segments (Root Levels) to Spinous Processes.—A number of researches dealing with the problem are available. In general it may be said that in the cervical region of the vertebral column the ordinal numeral of the spinous process is to be increased by one in order to give the ordinal numeral of the cervical nerve root arising at the level of that spinous process. In the region of the thoracic vertebræ two is to be added to the number of the spinous process in the upper half, while from the sixth to the eleventh thoracic vertebræ one must add three. The lower part of the spinous process of the eleventh thoracic vertebra and the interspace between this spine and the next lower corresponds to the origin of the third to the fifth lumbar roots; the spinous process of the twelfth thoracic vertebra and the interspace between it and the spinous process of the first lumbar vertebra correspond to the origin of the sacral roots. It is to be remembered that when the trunk is strongly flexed, the spinal cord with attached nerve roots is displaced a few millimeters upward.

The levels of the nerve roots differ somewhat in the child from those in the adult, as Chipault has pointed out. Thus in children under seven years of age we add three to the ordinal numeral for the spinous process in the region of the first four thoracic vertebræ to get the number of the nerve root of corresponding level; and in the region of the fifth to ninth thoracic vertebræ four must be added.

The lower level of the dural sac in the adult corresponds about to the level of the spinous process of the first sacral vertebra.

The topographical relations between the spinous processes and the roots of the spinal nerves are well shown in the accompanying figure copied from Reid (Fig. 4559).

Cauda Equina.—Exact measurements have been made in an eighteen-year-old individual of the distances between the root origins of the lumbar and sacral nerves and their foramina intervertebralia of exit by Testut. The distances measured are as follows:

N. lumbalis I	114 mm.
N. lumbalis II	138 mm.
N. lumbalis III	151 mm.
N. lumbalis IV	163 mm.
N. lumbalis V	181 mm.
N. sacralis I	188 mm.
N. sacralis V	280 mm.

The filum terminale measures sixteen centimeters in length and extends from the third lumbar vertebra to the second coccygeal vertebra.

Length of Different Portions of the Cord.—Ravenel gives the following measurements:

	In the male.	In the female.
Pars cervicalis	9.9 cm.	9.6 cm.
Pars thoracalis	26.2 cm.	22.9 cm.
Pars abdominalis	5.1 cm.	5.7 cm.
Pars pelvina	3.6 cm.	3.1 cm.

The thirty-one segments corresponding to the thirty-one pairs of nerve roots have been carefully measured in six individuals by Lüderitz (for the figures his original article is referred to). The longest segment is found about the middle of the pars thoracalis and corresponds to the fifth, sixth, seventh, or eighth N. thoracalis. The shortest segment usually pertains to one of the lowermost Nn. sacrales. The difference in length of segments is dependent upon growth relations. The length of the segments increases steadily from the lower part of the sacral cord up to the middle of the pars thoracalis, the increase being at first slight, between the individual segments, but higher up it is greater. The length of the segments then diminishes until the lowermost portion of the pars cervicalis is reached. In the latter the segments measure about alike, though there are slight variations.

Weight of the Spinal Cord.—The spinal cord weighs on the average from 27 to 28 grams, with considerable individual variation. The weighings of Meckel are of interest. For the three months' fetus, 0.12 gram (= $\frac{1}{8}$ of brain weight); for the five months' fetus, 0.36 gram (= $\frac{1}{68}$ of brain weight); for the nine months' fetus, 2.7 grams (= $\frac{1}{107}$ of brain weight); for a five months' child, 5.4 grams.

The relative weight of the human spinal cord compared with the body weight is as 1:1849.5 in the adult; in the new-born as 1:851.4. The relation of the human spinal cord weight to body weight in a whole series of animals is given in Ziehen. Keith has made many such measurements. Ziehen also gives a long table in which the relative weight of the spinal cord to the brain weight in animals is given. It is smallest in man and increases in the animal series steadily downward until fish are reached. In the adult human being the relation has been variously estimated from as 1:19 to as 1:51.13. The latest figures are those of Mies, who gives the relative weight of the cord to the brain as 1:49.80 in the female and 1:51.13 in the male.

Central Canal.—The spinal cord is a hollow tube, whose lumen in the early embryo is very wide. In later development the originally thin walls are thickened and the diameter of the lumen (now called *canalis centralis*) is greatly contracted (Figs. 4573 and 4574).

The central canal is very often invisible in the adult. Its lumen may vanish for considerable distances. It is stated that the central canal may remain open in perhaps ten per cent. of the cases throughout its whole length. Headward it is continuous with the central canal of the medulla oblongata (fourth ventricle), while caudalward it can be followed as far as the middle of the filum terminale, where it ends blindly.

The form of the canal is usually circular or elliptical; in the latter case the longer diameter is most often sagittal. In the intumescentia cervicalis it is a transverse ellipse, and in the intumescentia lumbalis a dorsoventral ellipse.

The gray matter about it has a gelatinous appearance (*substantia gelatinosa centralis*) and is rich in neuroglia and derivatives of ependymal cells.

In the lower part of the conus medullaris the central canal is expanded to form a terminal ventricle (*ventriculus terminalis*). The dorsal wall of this expansion is so thin that some have erroneously assumed that the cavity is open into the dorsal median sulcus.

The Coverings of the Cord (*Meninges*).—The spinal cord is surrounded in the vertebral canal by three membranes known as the spinal meninges; they are continuous above with the cerebral meninges. These three membranes are known as the *dura mater spinalis*, the *arachnoidea spinalis*, and the *pia mater spinalis.*

The dura mater is the strongest of the three and most external. The pia mater is the most delicate and the most internal, being applied everywhere closely to the cord. Between the two is the delicate non-vascular arachnoid. Between the dura mater and the inner surface of the bony vertebral canal is a cavity known as the epidural cavity (*cavum epidurale*). Between the dura mater and the arachnoid is a space called the subdural cavity (*cavum subdurale*). More important, however, is the space between the arachnoid and the pia mater. This is the subarachnoid cavity (*cavum subarachnoideale*); it contains the cerebrospinal fluid (*liquor cerebrospinalis*).

The spinal dura mater (*dura mater spinalis*) extends from the foramen magnum to the level of the second or third sacral vertebra. It differs from the dura mater of the brain in that it splits into two layers, the outer one becoming continuous with the periosteum and ligaments of the vertebral canal, and the inner one forming the dura mater spinalis proper. The latter layer is the one usually referred to when the spinal dura mater is spoken of, but it must be remembered that the outer layer must be added to it to make it homologous with the dura mater encephali. In the space between the outer layer and the dura mater spinalis proper, that is in the cavum epidurale, there are fatty tissue and some plexuses of veins and lymph channels. The thickness of the dura mater spinalis in the adult averages 0.5 to 0.6 millimeter.

Some fibrous filaments from the anterior middle line of the dura run obliquely downward and ventralward to be inserted into the posterior longitudinal ligament of the spine. These are especially developed from the fourth lumbar vertebra downward, where they fuse to form a membrane, the so-called ventral sacrodural ligament (*ligamentum sacrodurale ventrale*).

The spinal dura mater forms a separate sheath for each of the two roots, the ventral root and the dorsal root, of each spinal nerve. These sheaths are continued upon the roots as far as the spinal ganglia, where they become lost in the connective tissue of the peripheral nerves and in the periosteum of the bones.

At its lower extremity the dura mater spinalis forms a sac which envelops the nerve roots of the cauda equina. This sac terminates at the level of the second or third sacral vertebra, but the dura mater is continued as a sheath closely applied to the filum terminale. This portion of it, a long, tough thread, called the filum duræ matris spinalis, is finally inserted upon the posterior surface of the os coccygis.

The dura mater spinalis is connected with the arachnoidea by means of the so-called subdural threads and with the pia mater by the denticulate ligaments (*ligamentum denticulatum*). The subdural threads are very fine and short, are connected with the outer surface of the arachnoidea, and usually carry blood-vessels. The ligamentum denticulatum is a membrane stretched out in a frontal or coronal plane between the dura mater and the pia mater, just midway between the ventral and dorsal surfaces of the cord; it passes between the ventral and dorsal roots of the spinal nerves. Its medial border is firmly attached to the pia mater. Its lateral border is toothed, the teeth being inserted at their summits into the dura mater midway between the exits of adjacent spinal nerves. Intermediate between the teeth the lateral edge of the membrane forms free arcades. The number of teeth varies from eighteen to twenty-three. In the cervical region the N. accessorius runs dorsally of the ligament.

The spinal arachnoid (*arachnoidea spinalis*) bounds the subdural cavity internally. It is to be noted that this is what is called by many anatomists the "visceral layer of the arachnoid;" below, it is reflected at the tip of the conus terminalis upon the dura mater to form the "parietal layer of the arachnoid" of various authors. This is why some writers call the cavum subdurale, situated between the parietal layer and the visceral layer of the arachnoid, the "arachnoid cavity." It is a serous cavity, like the pleura.

The arachnoid contains no blood-vessels; occasionally calcified plates are found in the membrane. The arachnoid is prolonged over the nerve roots, and over the summits of the teeth of the ligamentum denticulatum.

As a rule, it is very difficult to separate the arachnoid from the pia mater macroscopically. Key and Retzius describe the two together as the "meninx tenuis." These soft membranes, together, are also designated, the "leptomeninges," to distinguish them from the hard or tough membrane, the dura mater or "pachymeninx." If the visceral layer of the arachnoid be lifted carefully in the region of the cauda equina and cut through with fine scissors and then split longitudinally upward a little to one side of the median line, the space between the arachnoid and the pia mater, the subarachnoid cavity (*cavum subarachnoideale*), will be exposed. This space is not a free cavity, but really a communicating network of cavities, the walls of which are formed by delicate processes which extend between the arachnoidea and the pia mater. The meshes are filled with cerebrospinal fluid. It is this cavum subarachnoideale which is tapped in Quincke's lumbar puncture when the needle is introduced opposite the interspace between the third and fourth lumbar vertebræ.

The spinal pia mater (*pia mater spinalis*), a very delicate membrane, closely envelops the spinal cord. It sends a fold into the depth of the ventral median fissure and elsewhere is intimately adherent to the external surface of the cord. It is extremely rich in blood-vessels, for it is in this membrane that the arteries which supply the cord undergo multiple subdivision before penetrating into the substance of the cord. When the pia mater is pulled off the cord, a number of minute arteries and capillaries are always torn out of the white substance; many of these are so small, however, that they cannot be made out with the naked eye.

The Blood-vessels of the Spinal Cord (Fig. 4560).—The arterial supply of the spinal cord is derived from the vertebral arteries (*rami spinales Aa. vertebrales*), the ascending cervical arteries (*rami spinales Aa. cervicales ascendentes*), the dorsal rami of the intercostal arteries (*rami spinales Rr. dors. Aa. intercostales*), the dorsal rami of the lumbar arteries (*rami spinales Rr. dors. Aa. lumbales*), the iliolumbar arteries (*rami spinales Aa. iliolumbales*), and the lateral sacral arteries (*rami spinales Aa. sacrales laterales*).

Besides the rami spinales given off from the cervical portion of the A. vertebralis which pass through the foramina intervertebralia, each vertebral artery gives off a ventral spinal artery (*arteria spinalis ventralis*) (O. T., A. vertebrospinalis anterior), and a dorsal spinal artery (*A. spinalis dorsalis*) (O. T., A. vertebrospinalis posterior). The ventral spinal arteries of the two sides run medialward and caudalward and unite near the ventral median fissure somewhere between the foramen magnum and the level of the third cervical nerve. The trunk resulting from the fusion of the two, sometimes called the median anterior vertebrospinal artery (*A. vertebrospinalis ventralis mediana*), runs downward, unpaired on the ventral surface of the cord (not in the ventral median fissure), as far as the level of the fourth or fifth cervical nerve, where it ends by fusing with the *tractus arteriosus spinalis ventralis*, the unpaired ventral median trunk resulting from anastomoses between the various spinal rami which come to the cord at the levels of the nerve roots all the way down as far as the filum terminale.

The dorsal spinal artery given off by the vertebral artery is delicate, bends around the lateral margin of the medulla oblongata and runs downward near the nervus accessorius on each side. Having reached the level of the fourth or fifth cervical nerve, it fuses with the longitudinal trunk, known as the *tractus arteriosus dorsolateralis*. The latter is made up of ascending and descending branches of the spinal rami of the A. vertebralis, Aa. intercostales, lumbales, iliolumbales, and sacrales laterales.

Besides this tractus arteriosus dorsolateralis the dorsal spinal artery from the vertebral gives off segmental branches, the so-called penetrating arteries (*Aa. penetrantes*), which, passing medialward and joining with branches of the Aa. intercostales, give rise to another longitudinal trunk called the *tractus arteriosus spinalis dorsalis*. The latter does not run in the middle line, but runs lengthwise of the cord just behind the line of entrance of the dorsal roots. The tractus arteriosus dorsolateralis, on the other hand, runs ventral to and lateralward from the sulcus lateralis dorsalis or line of entrance of the dorsal roots.

The rami spinales of the rami dorsales of the Aa. intercostales, the rami spinales of the Aa. lumbales, the A. iliolumbalis, the A. sacralis lateralis, as well as of the A. cervicis ascendens all run through the intervertebral foramina. On passing through the foramen, each ramus spinalis gives off two delicate branches, one to the ventral root (*A. radicina ventralis*), the other to the dorsal root (*A. radicina dorsalis*), and then, near the spinal ganglion, usually divides into two branches, one going to the front of the cord (*ramus spinalis ventralis*), the other going to the dorsolateral surface of the cord (*ramus spinalis dorsalis*). It is to be noted that there is not a ramus spinalis for every nerve-root level; and further, that sometimes when a ramus spinalis is present, it does not divide into two branches but becomes entirely a ventral ramus or a dorsal ramus, more often the latter. Thus, according to Kadyi, there are, as a rule, eight large rami spinales ventrales and as many as sixteen or seventeen rami spinales dorsales. Among the rami spinales ventrales there is usually one which is much larger than the others; this is sometimes called the *A. magna spinalis*, or *A. radicalis magna*. It may be either on the left side or on the right side, and is most often found in the lower thoracic region at the level of the ninth, tenth, or eleventh thoracic nerve. These ventral spinal rami run medialward as far as the fissura mediana ventralis, and there divide into an ascending and a descending ramus. These ascending and descending rami fuse with those of adjacent levels, thus helping to form the general *tractus arteriosus spinalis ventralis* of Kadyi, which lies in the epipial areolar tissue in the cavum subarachnoideale.

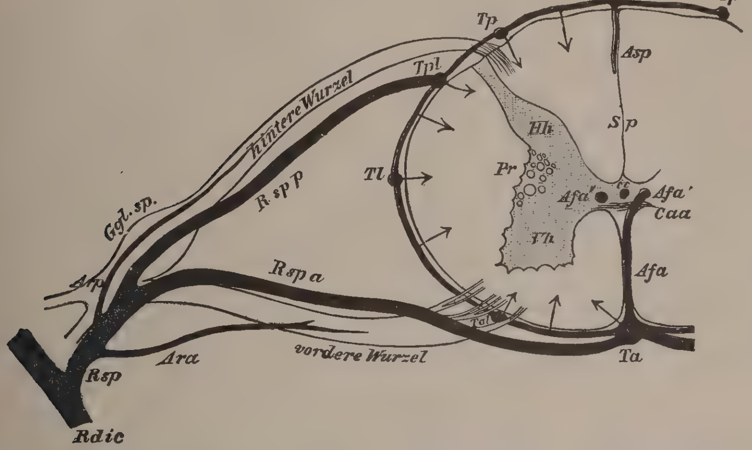

Fig. 4560.—Schematic Representation of the Arterial Vessels of a Segment of the Spinal Cord. For the sake of clearness the relative size relations of the vessels have been incorrectly drawn. *Afa*, Arteria fissuræ ventralis; *Afa'*, longitudinal central branch (ascending or descending) of *Afa*; *Afa''*, longitudinal central branch of the *Afa* next above or next below; *Ara*, arteria radicina ventralis; *Arp*, arteria radicina dorsalis; *Asp*, arteria septi mediana dorsalis; *Caa*, commissura ventralis alba; *Cc*, canalis centralis; *Ggl.sp.*, ganglion spinale; *Hh*, dorsal gray column; *Vh*, ventral gray column; *Pr*, processus reticularis; *Rdic*, rhombus dorsalis seu posterior arteriæ intercostales; *Rsp*, ramus spinalis; *Rspa, Rspp*, ramus spinalis ventralis, dorsalis; *Sp*, septum medianum dorsale; *Ta, Tal, Tp, Tpl*, tractus arteriosus ventralis, ventrolateralis, lateralis, dorsalis, dorsolateralis; *hintere Wurzel*, dorsal root; *vordere Wurzel*, ventral root. (After T. Ziehen, in Bardeleben's "Handbuch der Anatomie des Menschen," Jena, 1899.)

The dorsal spinal rami run also medialward to the surface of the cord, just in front of the line of entrance of the dorsal roots, and like the ventral spinal rami also divide into ascending and descending limbs, which, anastomosing with corresponding limbs of rami of adjacent levels, give rise to the longitudinal trunk known as the *tractus arteriosus dorsolateralis*. Other rami spinales dorsales run farther backward and medialward, pass between the dorsal roots of different levels, or among the fila radicularia of the dorsal roots to reach a position just medial from the sulcus lateralis dorsalis, where they divide into ascending and descending limbs, which contribute to another longitudinal anastomosis known as the *tractus arteriosus dorsalis*, to which the Aa. penetrantes from the A. spinalis dorsalis of the A. vertebralis has above been seen to contribute.

The tractus arteriosus dorsolateralis lies lateral from the dorsal root and outside the pia mater. The tractus arteriosus dorsalis lies medial from the dorsal root, but inside the pia mater. Between the tractus arteriosus dorsalis of one side and its fellow on the opposite side pass transverse anastomoses like the rungs of a rope ladder. These transverse rami are particularly noticeable opposite the cervical and lumbar enlargements.

About one-half a centimeter above the tip of the conus medullaris a large transverse anastomosing branch can be seen, connecting the tractus arteriosus dorsolateralis with the tractus arteriosus ventralis. The presence of this large branch, sometimes called the *ramus crucians*, explains why it is that fluid injected through the arteria spinalis magna may be distributed through the blood vascular network of the whole lower half of the cord on its dorsal surface.

The ventral spinal artery and the tractus arteriosus spinalis ventralis with which it is continuous give off two sets of branches. One set is central (*Aa. fissurales ventrales seu centrales*); the other set is lateral and peripheral (*rami laterales*).

The ventral fissural arteries (*Aa. fissurales ventrales seu centrales*), 200 to 269 in number, pass into the depth of the ventral median fissure and divide into two branches, one of the latter passing to the right, the other to the left. These branches go through the commissura ventralis alba to the gray substance. They are known as the sulcocommissural arteries (*Aa. sulcocommissurales*). They often divide into ascending and descending branches which supply the whole of the gray matter of both the ventral and dorsal gray columns, with the exception of the most peripheral part of the gray substance next to the white matter. The special branches going to the nucleus dorsalis are called the *arteriolæ columnarum Clarkii*.

The rami laterales go to the ventral roots and anastomose with the Aa. radicinæ ventrales; sometimes they form a longitudinal anastomotic chain called the *tractus arteriosus ventrolateralis*. Other branches run backward to meet branches running forward from the tractus arteriosus *dorsolateralis* and to form a lateral longitudinal anastomosis known as the *tractus arteriosus lateralis*.

The whole of the white matter and the most peripheral part of the gray matter get their blood supply from branches penetrating the cord from the tractus arteriosus ventrolateralis, tractus lateralis, tractus dorsolateralis, tractus dorsalis, and the Aa. radicinæ ventrales et dorsales. All these vessels have been grouped together by Adamkiewicz, under the name vasocorona.

From the transverse anastomoses between the tractus arteriosi dorsales of the two sides, certain unpaired dorsal sulcal arteries (Aa. sulcales dorsales) penetrate into the cord in the region of the sulcus medianus dorsalis. These are much branched and supply the white substance, but scarcely go so deep as the dorsal commissure. Branches from them may, however, reach the dorsal gray column or the nucleus dorsalis, and help to contribute to the blood supply of those parts. Minute vessels, entering the white substance between the fasciculus gracilis (Golli) and the fasciculus cuneatus (Burdachi), tolerably constant in the upper portions of the cord, have been called the interfunicular arteries (*Aa. interfuniculares*). The branches of the Aa. radicinæ dorsales et ventrales which reach the interior of the cord are small, but they play some part in the vascularization of the ventral and dorsal gray columns.

The arteries supplying the spinal cord are *end arteries* in the sense of Cohnheim. This is true of all the branches going in from the vasocorona as well as of the branches of the Aa. sulcales ventrales et dorsales. This explains the possibility of minute infarctions in the spinal cord. Despite the manifold longitudinal anastomoses throughout the whole length of the cord between the arteries of all levels, the cutting off of the blood supply through the lumbar and sacral vessels leads irrevocably to the death of the gray matter of the lower part of the cord, as has been over and again demonstrated by the experiment in which the abdominal aorta is compressed for half an hour.

The capillaries of the cord empty into the veins which form a network in the pia. Out of this network several large veins become differentiated, and these have been given special names. Thus, on the ventral surface of the cord are found: (1) *V. spinalis mediana ventralis;* (2) *V. spinalis lateralis ventralis dextra;* (3) *V. spinalis lateralis ventralis sinistra.* On the dorsal surface of the cord a median and two lateral veins can also be made out: (1) *V. spinalis mediana dorsalis;* (2) *V. spinalis lateralis dorsalis dextra;* and (3) *V. spinalis lateralis dorsalis sinistra.*

All these veins are devoid of valves. They empty through the *Vv. spinales ventrales et dorsales* largely into the *plexus venosi vertebrales interni,* and partly through the *Vv. intercostales* into the *V. azygos.* Some of the veins pass by way of the *Vv. lumbales* into the V. cava inferior. Other veins go by way of the *V. iliolumbalis* and the *Vv. sacrales laterales* into the V. hypogastrica, and so through the V. iliaca communis into the V. cava inferior.

The veins from the gray matter empty largely through the *Vv. fissurales ventrales* into the V. spinalis mediana ventralis.

Fissures, Sulci, and Funiculi.—The external surface of the spinal cord is not perfectly smooth. There is a deep longitudinal groove on the ventral or anterior surface, the ventral median fissure (*fissura mediana ventralis*). In the median line on the dorsal or posterior surface there is no such deep groove, but only a shallow sulcus called the dorsal median sulcus (*sulcus medianus dorsalis*). The ventral spinal roots leave the spinal cord along a longitudinal area situated a little lateralward from the ventral median fissure; though there is in reality very little if any depression on the surface at the points of exit of the ventral rootlets, a shallow groove has been described here and designated the ventral lateral sulcus (*sulcus lateralis ventralis*). More dorsally, a few millimeters laterally of the dorsal median sulcus on each side and corresponding to the line of attachment of the dorsal rootlets, there is a distinct groove called the dorsal lateral sulcus (*sulcus lateralis dorsalis*).

These longitudinal sulci, running the whole length of the cord, subdivide its surface into strands which are known as *funiculi.* Of these funiculi, there are three for each half of the cord. Thus, between the ventral median fissure and the ventral lateral sulcus is situated the ventral funiculus (*funiculus ventralis*); between the ventral lateral sulcus and the dorsal lateral sulcus of the same half of the cord is situated the lateral funiculus (*funiculus lateralis*); and, finally, between the dorsal lateral sulcus and the dorsal median sulcus is situated the dorsal funiculus (*funiculus dorsalis*). In the upper part of the spinal cord the dorsal funiculus on each side is further subdivided by an additional sulcus known as the dorsal intermediary sulcus (*sulcus intermedius dorsalis*). The lateral portion of the dorsal funiculus included between the dorsal lateral sulcus and the dorsal intermediary sulcus is known as the wedge-shaped fasciculus (*fasciculus cuneatus*). The medial portion, situated between the dorsal intermediary sulcus and the dorsal median sulcus, is known as the slender fasciculus (*fasciculus gracilis*).

The Spinal Nerves.—Besides the fila radicularia of the dorsal and ventral roots of the spinal nerves, there can be made out in the uppermost part of the spinal cord a few fila radicularia coming off from the lateral surface between the ventral and dorsal lateral sulci; these unite to form on each side a nerve trunk which passes upward in the vertebral canal to enter the cranial cavity through the foramen magnum. These fila radicularia belong to the so-called accessory nerve (*N. accessorius*) or eleventh cerebral nerve.

Since the time of Sir Charles Bell, it has been customary to speak of the anterior or ventral roots as *motor roots,* of the posterior or dorsal roots as *sensory roots,* and of the spinal nerves resulting from the fusion of anterior and posterior roots as the *mixed nerve trunks* (see article *Cranial Nerves,* vol. iii., p. 321).

The mixed nerve trunk leaves the vertebral canal through the corresponding intervertebral foramen (*foramen intervertebrale*). In some parts of the cord the corresponding intervertebral foramen lies in a horizontal direction from the fila radicularia of the nerve, but in other parts of the cord, owing to greater rapidity of growth at certain periods of development of the bony vertebral canal than of the spinal cord itself, the intervertebral foramina are situated at much lower levels than are the fila radicularia of the corresponding spinal nerves. The result is that certain of the spinal nerves follow a more or less markedly oblique course between the cord and the intervertebral foramina. When this course is very oblique a considerable extent of the spinal nerve may be included within the cavity of the vertebral canal. Particularly striking is the obliquity of course and long intravertebral extent of the lumbar and sacral nerves. Indeed, some of the latter follow almost a vertical course, enveloping the conus medullaris and the filum terminale as a great bundle of nerves known as the horse's tail (*cauda equina,* Fig. 4557).

There are thirty-one pairs of spinal nerves, connected with the spinal cord. The spinal nerves are named according to their exit from the vertebral canal. The uppermost spinal nerve leaves the vertebral canal between the atlas and the os occipitale. All other spinal nerves come out through the intervertebral foramina between adjacent vertebræ, the lowermost one making its exit through the opening between the first and second portions of the os coccygis. It is customary then to divide the spinal nerves into cervical nerves (*Nn. cervicales*), thoracic nerves (*Nn. thoracales*), lumbar nerves (*Nn. lumbales,*) sacral nerves (*Nn. sacrales*), and coccygeal nerve (*N. coccygeus*). There are eight cervical nerves, twelve thoracic nerves, five lumbar nerves, five sacral nerves, and one coccygeal nerve. The portion of the spinal cord connected with the cervical nerves is known as the cervical part (*pars cervicalis*). The portion of the cord connected with the thoracic nerves is known as the thoracic part (*pars thoracalis*). The portion of the cord connected with the lumbar and upper sacral nerves is known as the lumbar part (*pars lumbalis*). That portion of the cord which is below the pars lumbalis is called the conus medullaris. The pars cervicalis includes the intumescentia cervicalis; the pars lumbalis includes the intumescentia lumbalis.

The Spinal Nerve Roots.—The ventral roots are composed entirely, or nearly so, of myelinated fibers which are axones of the neurones of the ventral gray column of the same side of the cord. They are exclusively efferent in function, and in general are of larger caliber than those of the dorsal roots.

Accurate counts of all of the myelinated fibers in the ventral and dorsal roots of a man of middle age weighing 180 pounds have been made by Ingbert. In brief he has found:

1. The total area of the cross-sections of the dorsal roots of the left spinal nerves of a large man is 54.93 square millimeters.
2. The total number of myelinated nerve fibers in the dorsal roots of the left spinal nerves of the same man is 653,627.
3. There are on the average 11,900 myelinated nerve fibers to every square millimeter of the cross-sections of the dorsal roots of man.
4. There is a close relation between the areas of the cross-sections of the dorsal roots and the number of nerve fibers which they contain (see Fig. 4561).
5. The small fascicles of a dorsal spinal root in general contain nerve fibers of small caliber.
6. The number of nerve fibers per square millimeter of the cross-section may vary considerably in the different fascicles of the same dorsal spinal root.
7. About seventy-nine per cent. of the myelinated nerve fibers in the dorsal spinal roots go to innervate the dermal surface; and about twenty-one per cent. are sensory fibers distributed to muscles and other deep tissues. The afferent fibers of spinal ganglion origin passing in the rami communicantes are not separately considered in this estimate, but are classed with those passing to the deeper tissues.
8. One cutaneous nerve fiber in the dorsal spinal roots innervates on the average 1.08 square millimeters of the skin of the head and neck, 1.30 square millimeters of the skin of the arm, 2.45 square millimeters of the skin of the leg, 3.15 square millimeters of the skin of the trunk, and 2.05 square millimeters of the skin of the entire body. These estimates are based upon the assumption that all functional types of fibers distribute as a single class; for each additional class of fibers assumed to have an independent distribution we must increase the area proportionately.
9. The total area of the cross-sections of the ventral roots of the left spinal nerves of the same man is 26.50 square millimeters.
10. The ratio of the total areas of the ventral and dorsal roots is 1:2.07.
11. In the dorsal roots the areas of the cross-sections is predominantly a function of the number of fibers, while in the ventral roots the area of the cross-section of the roots is chiefly a function of the size of the fibers.
12. The total number of the myelinated fibers in the ventral roots of the left spinal nerves is 203,700.
13. The ratio of the number of fibers in the ventral and dorsal roots is 1:3.2.
14. The ratio between the number of fibers in the ventral and dorsal roots of man is 1:3.2 (Ingbert); of the white rat, 1:2.3 (Hatai); and of the frog, 1:1.2 (Birge). From this we may conclude that probably the relative sensory supply increases as we ascend in the zoological series.

Some of the preceding data are summarized in the accompanying curves (Fig. 4561). It should be borne in mind that these enumerations include the myelinated fibers only and that in the dorsal roots there are probably more unmyelinated than myelinated fibers (Ranson).

The Spinal Ganglia.—The spinal ganglia contain the cell bodies of all afferent fibers which enter the spinal cord. The axones of these cells comprise the dorsal spinal roots. In birds and some other vertebrates efferent fibers (probably of visceral type), arising within the spinal cord, go out by way of the dorsal roots as well as by the ventral roots. The presence of such fibers in mammals is in controversy and their function is unknown, for physiological experiments have yielded no evidence of their presence.

The spinal ganglion is very complex with many different forms and sizes of cells. Its structure suggests that it might well serve as a correlation center for some types of reflexes, especially of the visceral systems, but as yet no physiological evidence of such functions has been adduced. Its neurone bodies certainly serve as the trophic centers for the fibers of the peripheral sensory nerves.

It has long been known that the number of neurone bodies in each spinal ganglion is more than twice as great as the number of myelinated afferent fibers entering the ganglion from the peripheral nerve. Moreover, the spinal ganglion cells are of two sorts, large and small, and the latter are the more numerous. Ranson has shown that more than half of the afferent fibers of the peripheral nerves related to the spinal ganglia are unmyelinated and that these latter fibers are the axones of the small cells of the spinal ganglia. These unmyelinated fibers have been neglected in all previous statistical work on the spinal nerves.

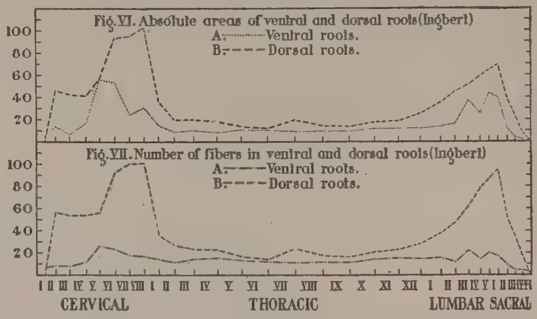

FIG. 4561.—Curves Showing (Fig. VI) the Absolute Areas of the Cross-section of the Ventral and Dorsal Roots of the Left Spinal Nerves; each sq. mm. is represented by 20 divisions on the axis of ordinates; (Fig. VII) the number of myelinated nerve fibers in the ventral and dorsal roots of the left spinal nerves; each 1,000 nerve fibers represented by 2 units on the axis of ordinates. (Ingbert, Journ. Comparative Neurology.)

The most generalized form of adult spinal ganglion cell has an oval body, from which arises a single stout process which is intricately coiled and while still within the ganglion divides into centrally and peripherally directed processes which enter the dorsal root and the peripheral nerve respectively. The variations of this form are innumerable, some of which are seen in Fig. 4562.

A few neurones of the spinal ganglion retain the embryonic bipolar form (Fig. 4562, 8). Some also show the generalized unipolar form described in the last paragraph (Fig. 4562, 1), though this is not the most numerous type. Many of these neurones give off collateral branches which terminate within the ganglion, around the body of either the cell of origin (Fig. 4562, 2) or of some other cell (Fig. 4562, 3), or the collateral branch may end free in the connective tissue within the ganglion (Fig. 4562, 3). Some of these collaterals end by specially elaborated terminal skeins which resemble the cutaneous sense organs of touch. These are especially numerous about the periphery of the ganglion and in the dorsal root. There are also unipolar cells whose single process divides T-form, but the peripheral division does not leave the ganglion (Fig. 4562, 7). These intraganglionic endings may take various forms resembling sense organs, as in the last case, and Dogiel is of the opinion that they are really sense organs and that the ganglion is therefore sensitive to pressure or other stimuli. In other cases the process of the unipolar cell may divide and reunite several times (Fig. 4562, 4), or several processes may arise from the cell body and then unite into a single fiber (Fig. 4562, 5). Other cells are truly multipolar (Fig.

4562, 9). Many variations of these forms have been described by Dogiel, Ramón y Cajal, and others.

Most of the neurones of the spinal ganglion belong to the somatic sensory system for either cutaneous or deep sensibility; but some of them are known to send their peripheral processes into the sympathetic nerves through the communicating branches. Moreover practically all of the cell bodies of the neurones of the spinal ganglion are said by Dogiel to be enveloped by a mesh of very fine unmyelinated fibers which enter the ganglion through the communicating branches from the sympathetic system, thus putting the entire visceral apparatus into the most intimate functional relation with the somatic sensory neurones of the spinal nerves (Fig. 4562, 1, 2, 3). The details of this sympathetic influence upon the somatic sensory neurones have never been worked out physiologically; but it is evidently of the utmost importance. This arrangement is probably one of the factors in the complicated clinical phenomena of referred pains. Visceral stimuli are known to exert a profound effect upon the subconscious as well as upon the conscious life, and much of that which we call temperament, mood, etc., may perhaps be traced in part to this factor.

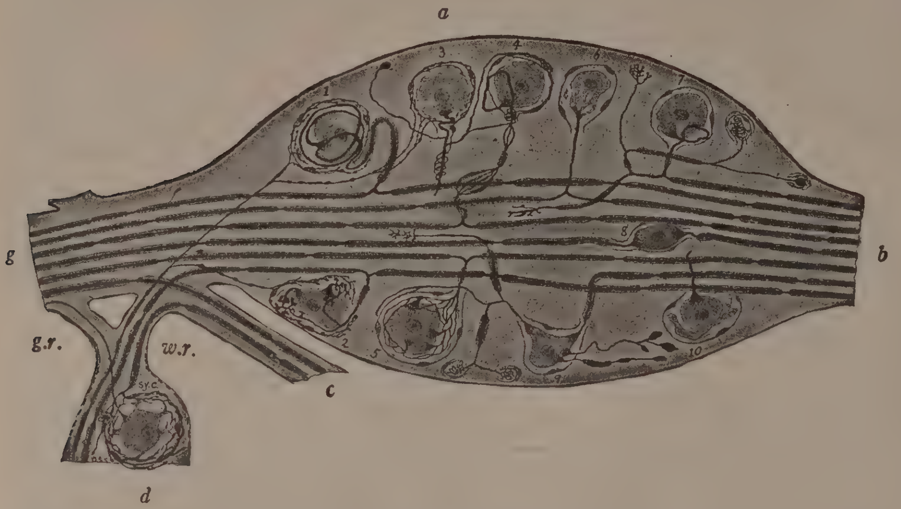

Fig. 4562.—Various Types of Neurones and Nerve Terminations found in a Spinal Ganglion. *a*, Spinal ganglion; *b*, dorsal root; *c*, ventral root; *d*, sympathetic ganglion; *g*, spinal nerve; *g.r.*, gray ramus communicans; *sy.c.*, neurone of sympathetic ganglion; *w.r.*, white ramus communicans. (Schematized from Dogiel, from Bailey's Histology.)

Topographical Relations of Gray Matter and White Matter.—If the spinal cord be cut through at different levels, it will be seen to contain a central canal (*canalis centralis*) and to be made up of gray matter (*substantia grisea*) and white matter (*substantia alba*). In general, the white matter is outside and the gray matter inside, and the latter in a transverse section assumes more or less the shape of the letter H; but the relations which exist between the white matter and the gray matter vary somewhat at different levels of the spinal cord.

A most valuable contribution to our knowledge of the details of these relations is to be found in Bruce's "Atlas of the Human Spinal Cord." It includes photographs of transverse sections through every segment of the cord. It is of the greatest convenience in helping to localize the origin of transverse sections of the human cord of unknown level.

Exact measurements of the surface amounts of the white and gray substances at different levels of the cord have been made by Stilling, who even went so far as to measure the surface areas of the individual funiculi at nearly all levels of the cord. Stilling's book on the spinal cord is a mine of valuable statistics.

In Stilling's book (1859) there are data concerning the areas of white and gray substance in cross-sections of the spinal cord of a child of five years, and these data were later used by Woroschiloff (1874) for the construction of curves. His curves are those at present employed in most text-books, too often without any accompanying statement to show that they are based on the measurement from an immature cord. Another point to be borne in mind in dealing with curves representing the true relations between the gray and the white matter is this, that the segments of the cord should be represented in their true length. The curves worked out by Krause and Aguerre would have been more valuable had they paid attention to the lengths of the segments.

Donaldson and Davis have constructed curves in which not only the area of the entire section, but also those of the white matter and the gray matter separately are represented, and in which the age of the individual and the true lengths of the individual segments of the spinal cord have been regarded. The accompanying charts make clear at a glance the results obtained (Fig. 4563). Donaldson and Davis find that the form of the cord from one to five years is nearly like that of maturity, the difference being that in the mature cord the relative enlargement of the areas of the cross-sections has become greater in the thoracic region, but less in the sacral and coccygeal. At maturity the relative enlargement of the two intumescentiæ is practically the same as at the fifth year. From the fifth year to maturity both the length and the weight of the entire cord, as well as the area of the cross-sections at the level of the several segments, are increased. The sum of the areas of the white substance at maturity is ninety-eight per cent. greater than at five years, and that of the gray substance twenty-three per cent. greater. This absolute increase must represent either enlargement of elements already completely developed or the development of elements still immature at the earlier age, or some combination of both these processes. Yet the failure of the intumescentiæ to increase in their relative area in the mature cord or in their proportional length would seem to indicate that during this period there was no increase in their relative complexity, a result which, to say the least, was unexpected.

The White Matter of the Spinal Cord.—The white matter of the ventral and lateral funiculi of the spinal cord shows in normal specimens no clearly marked subdivisions; but in the dorsal funiculus there is, as has already been mentioned, a dorsal intermediate sulcus or a connective-tissue septum (dorsal paramedian septum) marking the position of this sulcus, which separates the median fasciculus gracilis from the more lateral fasciculus cuneatus. These fasciculi are made up chiefly, though not exclusively, of the central courses of fibers of the dorsal roots, which are so arranged that those from the sacral parts of the cord lie nearest the dorsal median sulcus and those from higher levels are successively added laterally of these, an arrangement which is diagrammatically indicated in Fig. 4592.

There is considerable confusion in the terminology employed in the analysis of the spinal white matter, and the usage which follows differs in some respects from most of the current descriptions, no two of which agree among themselves. As already stated, the white matter of each half of the cord is divided topographically by the emerging spinal nerve roots into three funiculi.

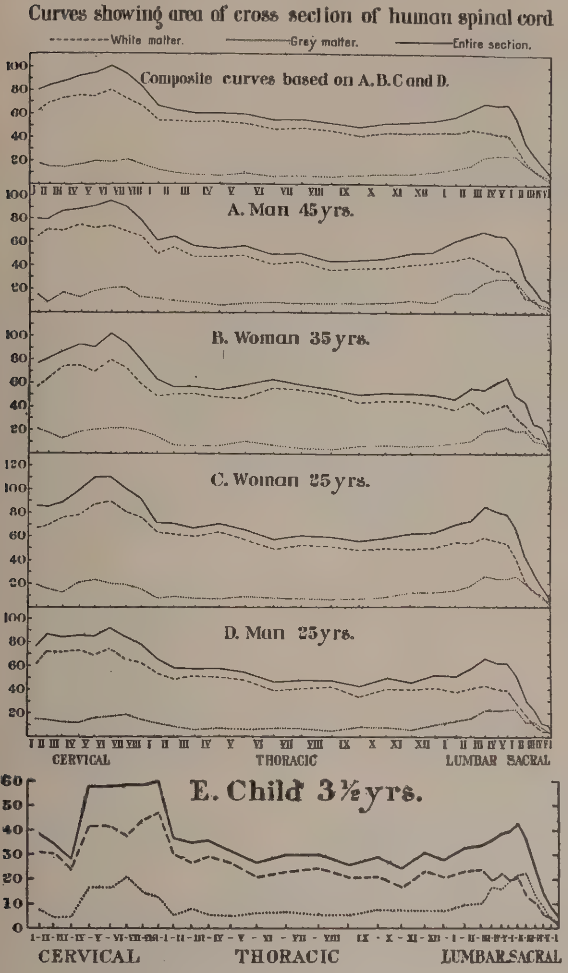

FIG. 4563.—This chart represents, by curves, the areas of the cross-sections of several human spinal cords, as well as the areas of the gray and white substances as they appear in each section. The base line in all the charts represents the length of the spinal cord for which it stands, and is divided into lengths proportional to those of the spinal-cord segments of which it is composed. On the ordinates one linear millimeter corresponds to one square millimeter of area. In all cases the measurement of the area was made at the caudal end of the segment. In the order from above downward, the curves are as follows:

Composite Curve—Based on *A*, *B*, *C*, and *D*, to give the average of the several areas in the curves named. The curves are generalized and apply to a cord of medium length—441.6 centimeters long. The influence of sex is neglected. The average age of the four cases would be thirty-three years. *Curve A*, Man of forty-five years; data for areas from Stilling. *Curve B*, Woman of thirty-five years; data for areas from Stilling. *Curve C*, Woman of twenty-five years; data for areas from Stilling. *Curve D*, Man of twenty-five years; data for areas from Stilling. *Curve E*, Child—data for areas from Stilling's observations on the cord of the two-year-old child. Length of segments from Lüderitz's observations on the cord of a three-and-a-half-year-old girl. Cord rather short. (After Donaldson and Davis.)

Each funiculus may be divided in a purely topographic sense into fasciculi, or collections of nerve fibers which occupy the same general region in the cross-section of the cord, such as the fasciculus gracilis of Goll and the fasciculus cuneatus of Burdach (which have already been mentioned as making up the greater part of the dorsal funiculus—see Fig. 4592) and the superficial ventrolateral fasciculus of Gowers (including among other tracts the spinal lemniscus and the ventral spinocerebellar tract of Fig. 4587). These fasciculi are usually mixed bundles containing tracts of diverse functional types. Neurologists formerly spoke of both funiculi and fasciculi as columns; but recent usage limits the use of the word column to the gray matter.

The nerve fibers of the white matter which lie nearest to the gray matter are for the most part relatively short and serve to connect various levels of the cord for the coordination of intrinsic spinal reflexes. These fibers in the aggregate are termed the *fasciculus proprius* (often called fundamental columns or ground bundles), and are separated into three divisions belonging in the several funiculi, viz., the fasciculus proprius ventralis, dorsalis, and lateralis. The more superficially placed fibers in general run longer courses and many of them connect the spinal cord with higher levels in the brain. The fasciculus proprius ventralis contains long fibers descending from the brain for motor coordination. In the medulla oblongata and midbrain these fibers form a compact bundle in the floor of the ventricle near the midplane known as the fasciculus longitudinalis medialis (old term fasciculus longitudinalis posterior, or posterior longitudinal bundle). In lower vertebrates many of the fibers of this system are of very large size (fibers of Müller), and in teleosts two of them attain to colossal size. These are the fibers of Mauthner, each of which arises from a giant cell in the medulla oblongata near the entrance of the vestibular root of the eighth nerve (see Bartlemez, 1915).

The number of myelinated fibers in various regions of the spinal cord has been estimated by Ziehen as given in the accompanying table.

Segments.	Ventral funiculus.	Lateral funiculus.	Dorsal funiculus.
Intumescentia cervicalis......	46,000	275,000	174,000
Midthoracic region..........	28,000	240,000	75,000
Intumescentia lumbalis......	42,000	260,000	85,000

The fibers of the ventral roots of the spinal nerves are all or nearly all myelinated; those of the dorsal roots contain myelinated and unmyelinated fibers, the latter in larger numbers (Ranson). The unmyelinated fibers for the most part enter the fasciculus dorsolateralis (Lissauer's bundle). This fasciculus has recently been shown by Ranson to be of mixed character, containing in the cat a lateral part of both myelinated and unmyelinated endogenous fibers probably belonging to the fasciculus proprius system and a medial part, also of myelinated and unmyelinated fibers which are derived from the contiguous dorsal roots. In the latter group the unmyelinated fibers predominate and Ranson is of the opinion that these fibers terminate in relation with the neurones of the gelatinous substance of Rolando of the dorsal gray column.

Most of the myelinated fibers of the dorsal roots enter the dorsal funiculus (fasciculus gracilis from the lower levels of the cord and fasciculus cuneatus from the upper levels (see Fig. 4592), within which they course for longer or shorter distances. These fibers divide into ascending and descending branches, the descending branches passing downward for only a few segments, while the ascending branches may extend for the entire distance from the point of entrance to the upper end of the cord (Figs. 4582 and 4591).

The true units of the spinal white matter are the *tracts, i.e.* collections of nerve fibers of similar functional type and connections. These tracts by some neurologists are termed fasciculi, and, like the other tracts of the central nervous system, they are in general named in accordance with the terminal relations of their fibers, the name of the location of their cells of origin preceding that of their place of discharge in a hyphenated compound word. Thus, the tractus rubro-spinalis arises from cells of the nucleus ruber of the midbrain and terminates in the spinal cord, and the tractus spino-cerebellaris arises in the spinal cord and terminates in the cerebellum. But, as already stated, there is no uniformity in the nomenclature of these tracts and no two authorities agree exactly in the terminology adopted. Moreover, few of the tracts have clearly defined anatomical limits, in most cases the fibers of different systems being more or less mingled.

The Gray Matter of the Spinal Cord.—The gray matter of the spinal cord, when examined in cross-section, is seen on each side to consist of a slender dorsal horn and a more massive ventral horn. When the third dimension is considered these represent longitudinal gray columns (*columna dorsalis grisea* and *columna ventralis grisea*), between which is an imperfectly separable intermediate zone and in some parts of the cord a distinct lateral column (*columna lateralis grisea*) (see Figs. 4565, 4566, and 4567). The dorsal column shows a constriction at its base, the neck of the dorsal column (*cervix columnæ dorsalis*). Near the tip (*apex*) of the dorsal column is an expanded mass of unusually transparent gray matter, the gelatinous substance of Rolando (*substantia gelatinosa Rolandi*). The dorsal column is separated from the surface of the cord by a strand of pale fibers, the fasciculus dorsolateralis or Lissauer's bundle. The ventral gray column is separated from the surface by wide masses of fibers of the ventral and lateral funiculi. In the angle between the dorsal and lateral gray columns is a network of white fibers and gray matter known as the reticular formation (*formatio reticularis*). Some of this tissue is found throughout the length of the cord, though it is more extensive in the cervical cord than elsewhere, where it is termed the *processus reticularis* (Fig. 4566).

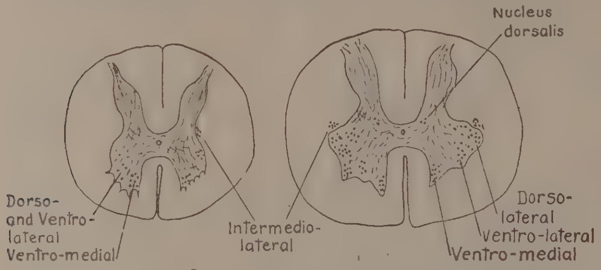

Fig. 4564.—Cross-sections through the Eighth Cervical Segment of Two Spinal Cords from New-born Infants, to illustrate the groupings of the neurones of the ventral gray columns in a normal child (on the right) and in a child in which both arms were entirely lacking (on the left). In the armless infant (abrachius) the ventromedial group is the same as in the normal, but the ventrolateral and dorsolateral groups are greatly reduced. (After Curtis and Helmholz.)

The nerve cells of the *dorsal gray column* are in general smaller than those in the ventral column. The gelatinous substance of Rolando contains an enormous number of very small nerve cells and very few neuroglia cells. Ranson is of the opinion that these cells are related to the unmyelinated fibers of the dorsal roots. The destination of their axones is unknown. Immediately internal to the gelatinous substance in the *caput* or head of the dorsal column is a region containing numerous myelinated fibers and scattered neurones of medium and small size (Figs. 4565 and 4566). The cells of this region (possibly including also those of the gelatinous substance) appear to serve as the second neurones in the conduction pathway for sensory impulses of touch, temperature, and pain and to send their axones into the ascending spinothalamic tracts of the opposite side of the spinal cord which in this article are called the spinal lemniscus (see Fig. 4587). The cells of the *cervix* or neck of the dorsal column, of the intermediate zone, and of the adjacent reticular formation are concerned chiefly with the intrinsic reflex connections of the spinal cord itself (see Figs. 4581 and 4583).

The nerve cells of the *ventral gray column* are for the most part large and the axones of these neurones form the ventral root fibers of the spinal nerves. They are arranged in groups which form longer or shorter subsidiary columns or nuclei, which are related to functional groups of muscles. Perfect agreement has not yet been reached regarding the exact pattern of this functional localization of the muscles. The anatomical arrangement is given with all desired fulness in Bruce's Atlas of the Spinal Cord, and in a later paper on the Intermediolateral Tract. In the latter work Bruce has shown that the neurones of the intermediolateral column, which in the thoracic and upper lumbar regions border the lateral column but do not form a part of it, are probably the cells of origin of the efferent preganglionic fibers which enter the sympathetic nervous system through the communicating branches (Fig. 4579).

The neurones of the ventral column proper are arranged in a ventromedial group, which runs the entire length of the cord with but small variations in size, and a number of lateral groups whose relations are very diverse in different regions. These lateral groups are greatly strengthened in the cervical and lumbar enlargements, and it is now commonly believed that they give rise to the motor fibers for the muscles of the limbs. This conclusion, so far as the innervation of the arms is concerned, has been strengthened by a case, recently reported by Curtis and Helmholz, who examined the spinal cord of an infant born without arms. Upon comparing a cross-section through the cervical enlargement of this spinal cord with that of a normal stillborn infant (Fig. 4564), it is evident that in the armless child the lateral groups of ventral column cells are greatly reduced in number, while the ventromedial groups are undiminished.

Sections of the Spinal Cord.—We shall next examine the appearances of transverse sections through the spinal cord at selected levels. A section through the middle of the cervical portion of the cord is illustrated in Fig. 4565. The ventral median fissure is broad and deep and contains a fold of pia mater containing blood-vessels. The dorsal median sulcus is deeper but not so broad; it contains no fold of pia mater and is in fact not a true fissure but is formed during embryological development by the coalescence of the lateral walls of the primitive neural tube, thus occluding the dorsal portion of its cavity.

The only nervous connection between the two halves of the cord is a narrow transverse band of nervous substance called the commissure. The ventral third of this commissure is composed of white matter and the dorsal two-thirds of gray matter In the middle of the gray commissure is the central canal (*canalis centralis*) of the spinal cord, lined by ependymal cells. The central canal divides the commissure into a ventral part (*commissura ventralis*) and a dorsal part (*commissura dorsalis*). The ventral commissure consists of white matter in front and gray matter behind. The dorsal commissure consists chiefly of gray matter, though some white fibers run through it. The dorsal median septum extends inward as far as the dorsal commissure, and the ventral median fissure likewise extends inward to the ventral white commissure.

Figure 4566 illustrates a cross-section through the cervical enlargement at the level of the sixth cervical segment. There is a notable increase in the size of the cord and a change of the gray matter. Both the dorsal and the ventral gray columns are considerably enlarged, and the ventral column has fused with the lateral column so that the latter does not appear at this level as a distinct column. The lateral diameter of the cord is increased much more than the vertical. The subdivision of the dorsal funiculus into fasciculus gracilis and fasciculus cuneatus is more evident here than at the higher level.

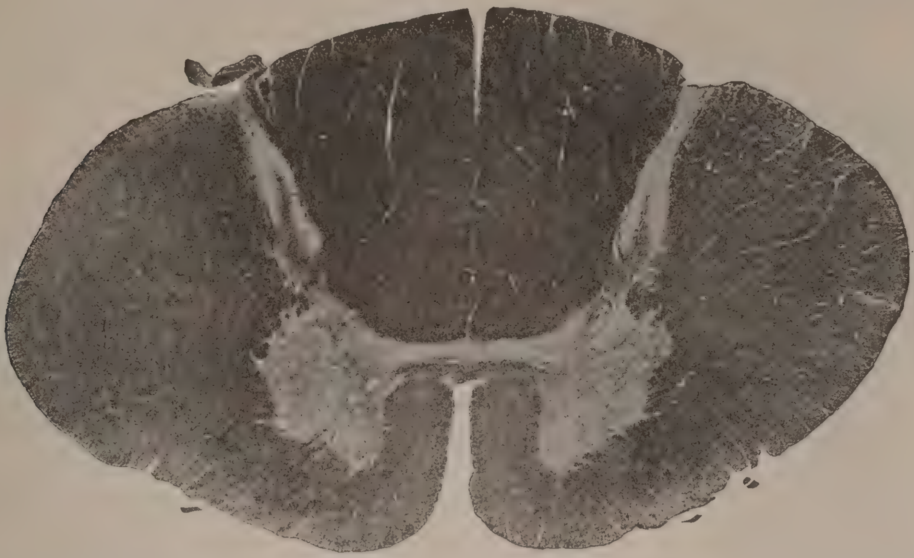

Fig. 4565.—Transverse Section, through the Fourth Cervical Segment of the Human Spinal Cord, the white matter colored dark by Weigert's myelin-sheath stain. (After A. Bruce, "Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

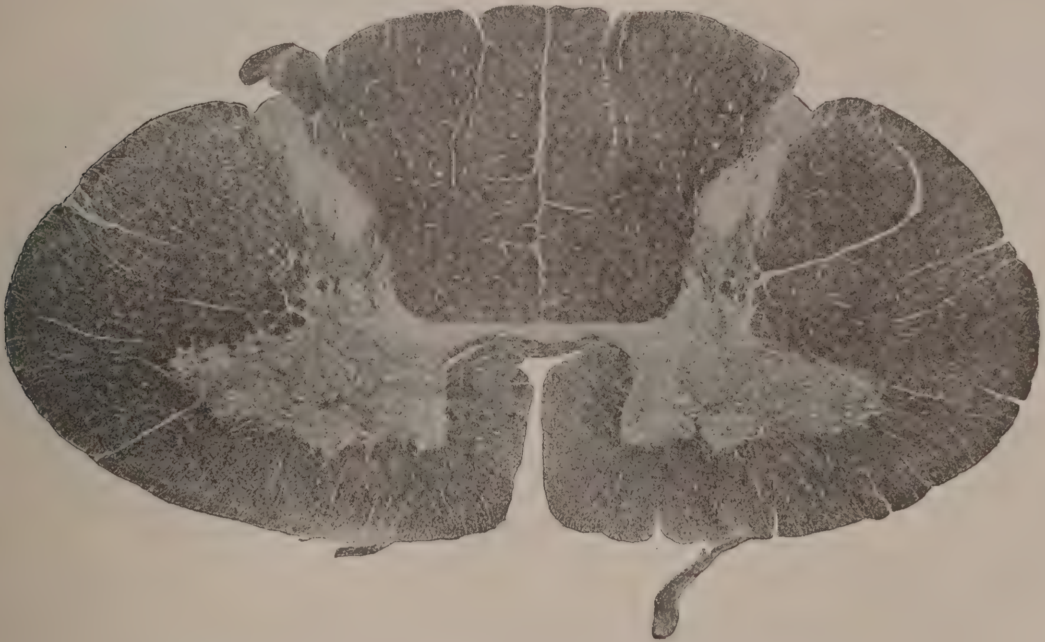

Fig. 4566.—Transverse Section through the Sixth Cervical Segment of the Human Spinal Cord. Weigert myelin-sheath stain. (After A. Bruce, "A Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

At the *level of the third thoracic nerve* (Fig. 4567) the size of the cord has become much reduced, and the vertical diameter is now much more nearly equal to that of the transverse diameter. The gray matter is present in much smaller amount, the ventral column has been greatly reduced in size, the lateral column is small, and the dorsal column slender and long. On the medial side of the dorsal column, just in front of its neck in the angle formed by it with the gray commissure, there is an expansion of the gray matter which was not visible in the two sections previously examined. This mass of gray matter contains large cells and is known as the dorsal nucleus of Clarke (*nucleus dorsalis* [*Clarkii*]). It is sometimes known as the column of Clarke or of Stilling. It is present on each side for a long distance in the cord; thus it extends throughout the whole thoracic part of the spinal cord and into the pars cervicalis as far as the level of the eighth or seventh cervical nerve; below, it extends into the pars lumbalis as far as the first or second lumbar nerve. The beginner will find in it a useful landmark for the recognition of sections derived from the pars thoracalis.

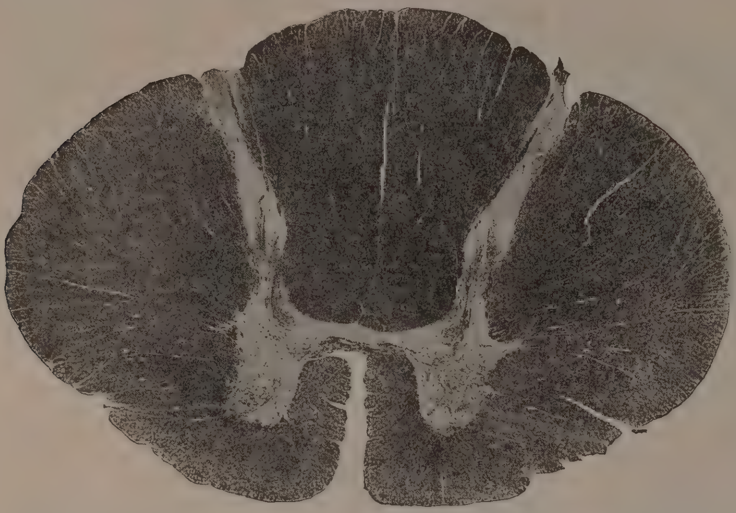

Fig. 4567.—Transverse Section through the Third Thoracic Segment of the Human Spinal Cord. Weigert's myelin stain. (After A. Bruce, "A Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

Sections of the thoracic cord below the eighth thoracic nerve show no marked alterations in the disposition of the white and gray matter until the lumbar enlargement (*intumescentia lumbalis*) is approached. Then the whole cord grows larger, both the gray matter and the white matter increasing in amount, the gray matter, however, to a greater extent than the white matter.

The relations at the *level of the fifth lumbar nerve* are well shown in Fig. 4568. The ventral and lateral columns of gray matter are again fused and form a much expanded mass in the ventral part of the cord. The dorsal column is enlarged to a greater extent here than in any other part of the cord. The enlargement involves especially its medial surface, with the result that the volume of the dorsal funiculus of the white matter is relatively small. Indeed, a striking feature of cross-sections through the lumbar enlargement is the thinness of the white envelope and the marked expansion of the gray matter. In the latter the substantia gelatinosa (Rolandi) is especially prominent.

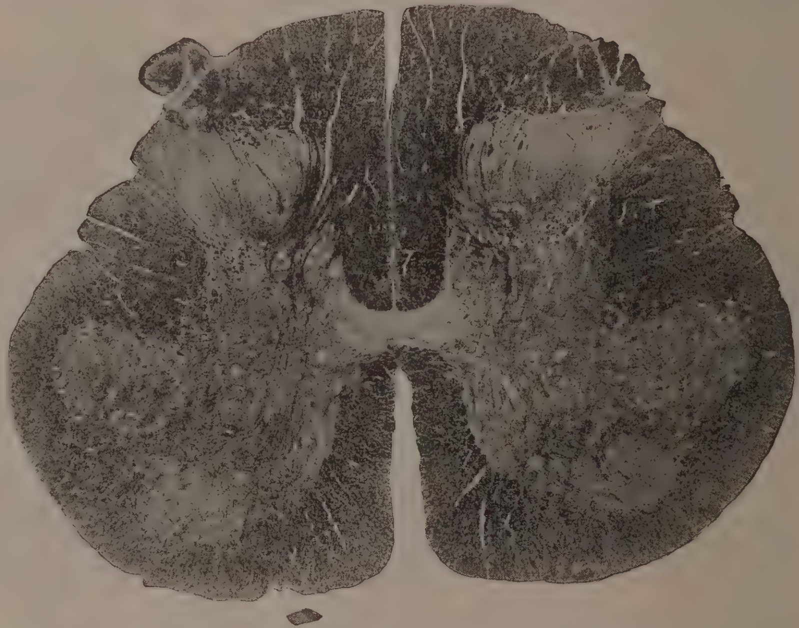

Fig. 4568.—Transverse Section through the Fifth Lumbar Segment of the Human Spinal Cord. Weigert's myelin-sheath stain. (After A. Bruce, "A Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

In the parts of the cord below the lumbar enlargement this disproportion between the volume of the gray matter and that of the white matter increases. A transverse section at the *level of the third sacral nerve* (Fig. 4569) shows this distinctly, and it is even more marked in a transverse section through the lower part of the conus medullaris at the *level of origin of the N. coccygeus* (Fig. 4570). Here the terminal mass of gray matter is surrounded by only a thin film of white matter. The filum terminale is so atrophic that sections of it reveal only the central canal, lined by ependymal epithelium and surrounded by a thin layer of gray substance, and outside of all the filum duræ matris spinalis.

Development.—The histogenesis of the spinal cord has been briefly reviewed in the article *Brain Anatomy* (vol. ii., p. 281), the early stages of this process being essentially similar in the spinal cord and brain. In the spinal cord of a human embryo of 6.9 millimeters (about four weeks) the nuclei of all of the cells are crowded together toward the ventricular surface, leaving a non-nucleated marginal layer next to the meningeal membrane (Fig. 4571). But already at this age many of these nuclei have begun to migrate outward, thus forming a *mantle layer* of more loosely arranged nuclei. The cells represented by the nuclei of the mantle layer are *neuroblasts*, or immature neurones. The neuroblasts in the ventral part of the neural tube develop more rapidly than those in the dorsal part, and many of these become neurones whose axones form fibers of the ventral roots of the spinal nerves. The remaining neuroblasts of the ventral part and all of those of the dorsal part become neurones devoted to internal adjustment, whose axones do not leave the spinal cord.

During or immediately after the closure of the neural tube a longitudinal strand of cells is separated from it to form the *neural crest*, whose development is very briefly summarized in the article *Cranial Nerves* (vol. iii., p. 326). The cells of the neural crest have very diverse histories. Some are transformed into the neurilemma sheaths of the peripheral fibers of the dorsal roots (Harrison), some migrate peripheralward to form neurones of sympathetic ganglia, and many remain to form neurones of the spinal ganglia.

The immature spinal ganglion cells, like those of the cranial ganglia (see vol. iii., p. 330), are at first bipolar, a dendrite and an axone arising from opposite poles of the cell body. They are later transformed into unipolar neurones by the approximation of the two processes and their final fusion for a part of their courses. Fig. 4572 illustrates the spinal ganglion of a chick embryo at the age exhibiting bipolar neurones. The peripheral process, which is a true dendrite, grows outward to come into relation with its appropriate receptor. The centrally directed process, or axone, grows inward, pierces the external limiting membrane of the spinal cord, and here bifurcates into ascending and descending branches. These nerve fibers form the beginning of the dorsal funiculus (Fig. 4572).

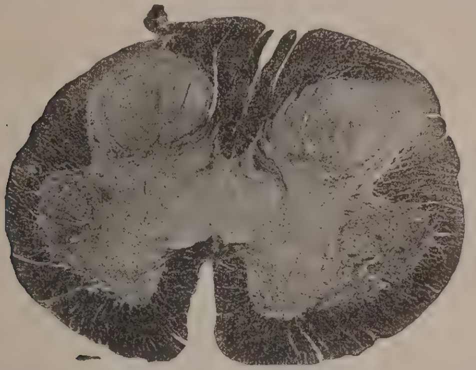

FIG. 4569.—Transverse Section through the Third Sacral Segment of the Human Spinal Cord. Weigert's myelin-sheath stain. (After A. Bruce, "A Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

In later development there is a further proliferation of neuroblasts and accumulation of neurones to form the dorsal, ventral, and lateral gray columns and an accumulation of nerve fibers peripherally to form the funiculi of white matter. There is, however, no proliferation of neuroblasts in the median line, thus leaving membranous longitudinal zones above and below the ventricle, the roof plate and the floor plate respectively (Fig. 4573).

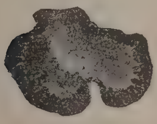

FIG. 4570.—Transverse Section through the Coccygeal Segment of the Human Spinal Cord. Weigert's myelin-sheath stain. (After A. Bruce, "A Topographical Atlas of the Spinal Cord," Edinburgh, 1901.)

The more rapid growth of the ventral gray columns and ventral funiculi causes a ventral projection on each side of the midplane separated by the ventral longitudinal fissure. The dorsal median sulcus is a very slight indentation of the dorsal surface, below which is a dorsomedian septum formed by a lateral compression of the dorsal part of the ventricle of the neural tube and fusion of the lateral walls (Fig. 4574).

Coghill has investigated the relations of the neurones in the spinal cords of amphibian embryos in the youngest stages which are capable of responding to external stimulation. In these embryos the earliest peripheral sensory neurones to mature are not those of the spinal ganglia, but a series of giant cells (first described by Rohon and Beard) within the spinal cord. In most vertebrate embryos these giant cells disappear after the neurones of the spinal ganglia have matured, though in some species, as in the marine goosefish (Lophius), they persist up to adult life.

It has been shown by Coghill that in Amblystoma the earliest somatic movements in response to external stimulation are possible only after the completion of a definite anatomical circuit in the nervous system (though the muscles may be excited to contraction by the direct application of an electrical stimulus prior to this age). The first movement which can be evoked by light tactile stimulation of the skin is a simple avoiding reaction—at first turning

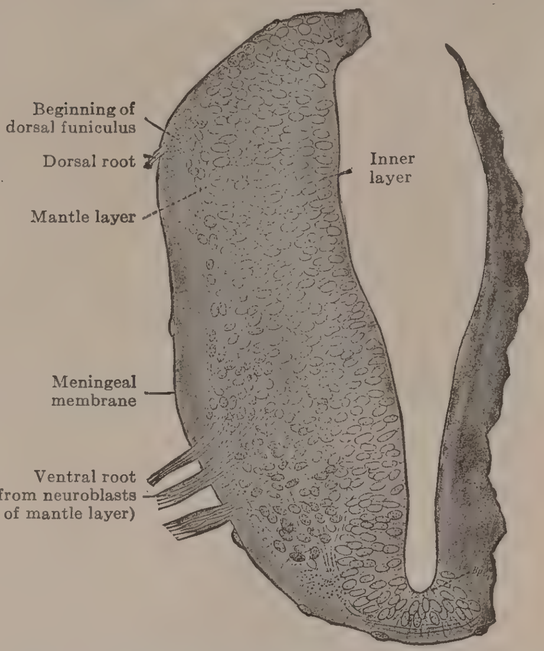
Beginning of dorsal funiculus
Dorsal root
Mantle layer
Inner layer
Meningeal membrane
Ventral root (from neuroblasts of mantle layer)

FIG. 4571.—Half of a Transverse Section of the Spinal Cord of a Four Weeks' (6.9 Millimeters) Human Embryo. *Dp.*, Roof plate; *Bp.*, floor plate. (After His.)

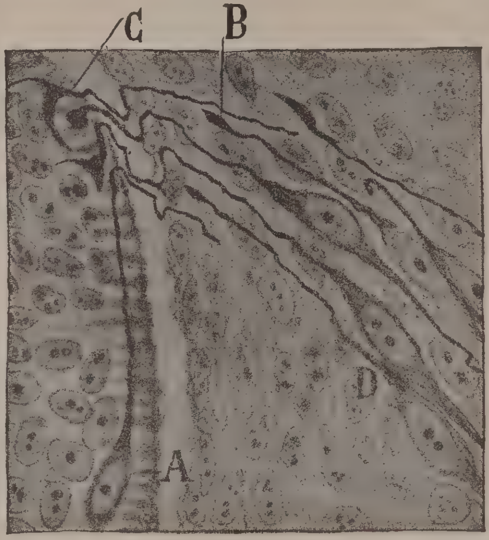

FIG. 4572.—Section through Part of the Spinal Cord and Spinal Ganglion of a Fifty-six-hour Chick Embryo (combined from two sections). *A*, Efferent neurone whose axone leaves by the dorsal root; *B*, cone of growth of central process (afferent dorsal root fiber) of spinal ganglion cell; *C*, bifurcation of afferent root fibers in the spinal cord, forming the beginning of the dorsal funiculus. (After Ramón y Cajal.)

the head end of the body away from the side stimulated, then a convulsive "coil reaction," then an "S-reaction," which is immediately followed by a true swimming reflex.

In the youngest stages which are capable of responding at all to external stimuli, commissural fibers cross at one region only, viz., the upper end of the spinal cord and lower end of the medulla oblongata. In older stages, this ventral commissure is extended both forward and backward from this level until finally it extends throughout the entire central nervous system below the optic chiasma, and other types of connection between the peripheral sensory and motor neurones are effected, so that local crossed and uncrossed reflexes are possible in every part of the central nervous system.

From these observations it follows that the earliest reflex responses to external stimulation require a rather complex chain of neurones, whose relations are quite different from those of the shortest definitive reflex arc of the adult animal.

In this arrangement we would emphasize the following features: (1) the fact that a single peripheral sensory neurone may be excited either by an exteroceptive stimulus applied to the skin or by a proprioceptive stimulus ("muscle sense") arising from the contraction of the myotom during the act of swimming; (2) the fact that the peripheral motor neurones are not yet separately differentiated away from those of the central motor tract; (3) that the reflex path required for the type of crossed reaction which is first to appear is a relatively long one, all of the afferent impulses having to reach the upper end of the spinal cord before they can be transferred across the midplane into the efferent apparatus; (4) that the individual neurones of this circuit are relatively short and that many synapses are interpolated in the pathway.

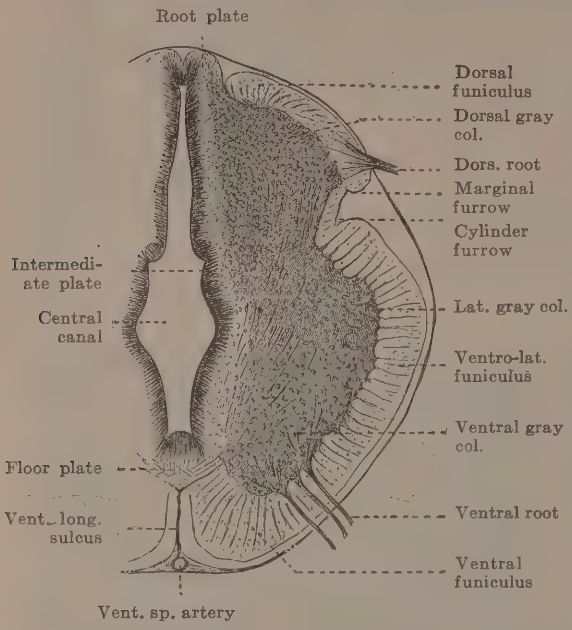

FIG. 4573.—Half of a Transverse Section through the Spinal Cord of a Human Embryo of 18.5 Millimeters (seven and one-half weeks). (After His.)

In the actual operation of this mechanism it appears that a bodily movement may be initiated by a single external tactile stimulus which is transmitted inward through the cutaneous dendrite of a dorsal giant cell (Figs. 4575 and 4576) and that this movement takes the form of a swimming reflex whose rhythm begins at the head end of the body and is transmitted backward through the myotomes of the side opposite to the one stimulated. The first stage in this movement is a bending of the head away from the side touched. This curvature of the body then moves backward, involving the successive contraction of additional myotomes, and after several myotomes of the upper part of the trunk have been involved, the muscular branches of the dorsal giant cells are excited by the contraction of their respective myotomes, thus exciting a proprioceptive reaction through the dendrites of the giant cells ending in the myotomes. This stimulus is likewise transmitted to the upper end of the spinal cord, passed over to the opposite side and into myotomes lying in front of those now in contraction. The effect is to turn the head to the opposite side and thus initiate a descending wave of muscular contraction which follows the first but in the opposite direction. This process is continued and repeated as long as the swimming movement persists, thus giving rise to the serpentine swimming reflex.

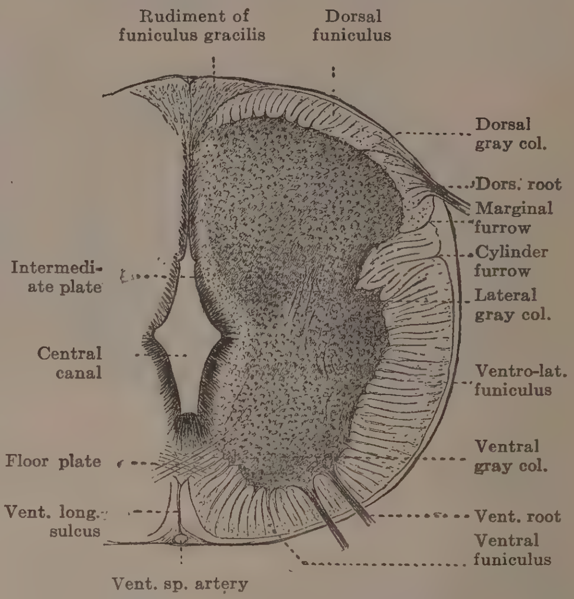

FIG. 4574.—Half of a Transverse Section through the Spinal Cord of a Human Embryo of Twenty-four Millimeters (eight and one-half weeks). (After His.)

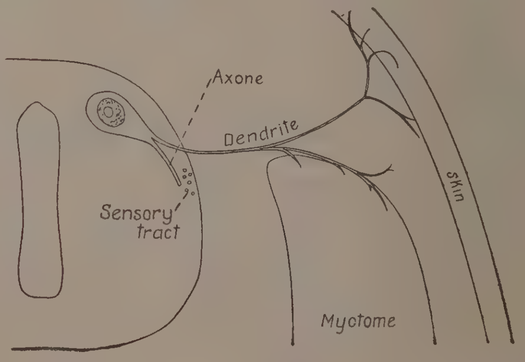

FIG. 4575.—Diagrammatic Cross-section through the Spinal Cord and Part of the Body of an Early Swimming Stage of Larval Amblystoma, to illustrate the connections of the transitory giant cells of Rohon-Beard. (Based on the researches of Coghill.)

This mechanism obviously is adapted to produce only one form of response to any sort of excitation applied to the trunk region of the embryo, viz., a swimming reaction, and the same neurones are involved throughout in both the exteroceptive and the proprioceptive factors in the reaction. Physiological experiments show that this in fact is the case.

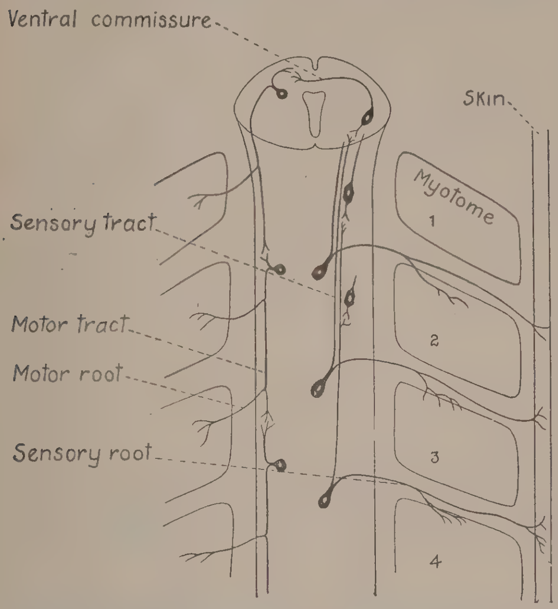

FIG. 4576.—Diagram of a Dorsal View of the Upper End of the Spinal Cord of Larval Amblystoma of the Same Age as in Fig. 4575, to illustrate the relations of the giant cells, commissural cells, and motor cells and the mechanism of the swimming reflex. (Based on the researches of Coghill.)

At a later period in development the transitory dorsal giant cells disappear and are replaced by typical spinal ganglion neurones which have meanwhile differentiated from the neural crest. And no doubt the adult Amblystoma, like the higher vertebrates, possesses distinct neurones within the spinal ganglia to serve the exteroceptive and the proprioceptive functions respectively involved on the afferent side of the swimming reflex.

In older larvæ the efferent side of the reflex circuit also shows an advance beyond that of the youngest swimming embryo, where the motor root fibers arise as collateral branches from the descending tract fibers. The details of the transformation have not been observed; but it is probable that in some of these neurones the descending tract fiber elongates and develops at the expense of the peripherally directed collaterals, while in others a collateral develops at the expense of the descending fiber, thus transforming the element into a typical ventral horn neurone.

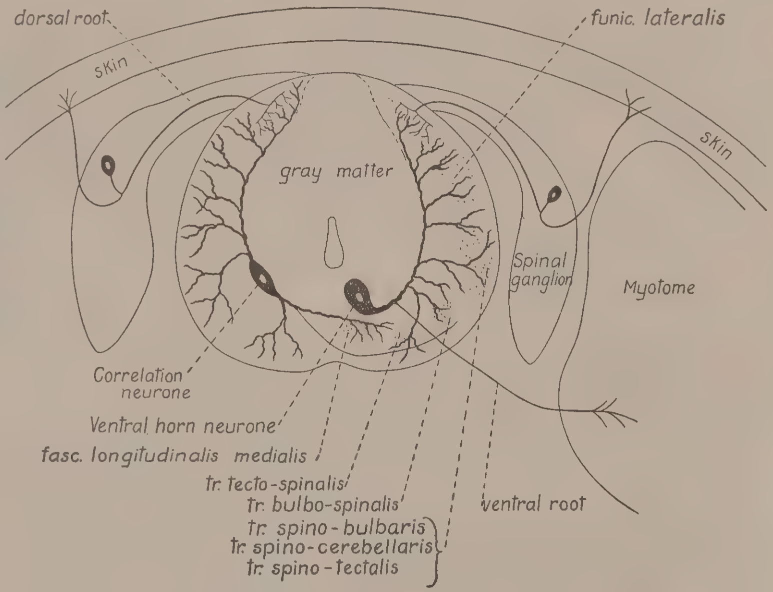

FIG. 4577.—Diagram of the Relations of Some of the Neurones of the Spinal Cord in a Half-grown Larva of Amblystoma. (After Herrick and Coghill.)

In the spinal cords of older larvæ this mechanism is much more complex than that of the earliest swimming larva, though still very different from that known in the spinal cords of adult higher vertebrates. The spinal ganglion cells and the ventral horn cells have fully matured and Fig. 4577 shows that both crossed and uncrossed reflex connections are possible at all levels of the spinal cord. Dorsal root fibers from the spinal ganglion neurones pervade the dorsal part of the white substance and the remainder of this layer is filled with various kinds of correlation fibers. Both the correlation neurones and those of the ventral horns send enormous dendrites into all parts of the cross-section of the white substance, some even crossing to the opposite side through the ventral commissure.

From these relations it is evident that each peripheral motor neurone is under the direct physiological influence of every sort of nervous excitation which can be transmitted through the spinal cord. These excitations may come from the skin of its own or of very remote segments of the body through dorsal root fibers, or they may come from the brain through the various cerebrospinal tracts—from the visual centers through the tractus tectospinalis, from the auditory or vestibular centers through the tractus bulbospinalis, etc. Furthermore, the long ascending systems between the spinal cord and the brain (spinobulbar, spinocerebellâr, and spinotectal tracts) may also discharge collaterals among dendrites of these peripheral motor neurones.

The Amblystoma larva is capable of making only the simplest responses by means of the body musculature, of which the chief is the simple swimming movement; but, unlike the younger embryos considered in the preceding paragraphs, these responses may be called forth by a great variety of means. The body musculature here is responsive to environmental influences received through many more avenues of sense, and its movements are, in addition, under the control of the higher correlation centers of the brain.

The functional connections of these exceedingly simple amphibian spinal cords forecast the histological pattern found in those of mammals. There is, first, an intrinsic apparatus of central adjustment adapted to serve the very simple total swimming movements which comprise the chief methods of response shown by these larvæ. In the second place, there are long ascending and descending fiber tracts which put this intrinsic apparatus into relation with the sense organs and higher correlation centers of the head.

In larval Amphibia there is a single ascending conduction system, some of whose fibers end in the medulla oblongata (tractus spinobulbaris), others in the cerebellum (tractus spinocerebellaris), still others in the roof of the midbrain (tractus spinotectalis, and a smaller number in the thalamus (tractus spinothalamicus, or spinal leminiscus). Some of the fibers terminating in the bulb and cerebellum arise as collaterals of the longer fibers of the spinal lemniscus. From this arrangement it would appear that these ascending fibers possess but little functional specificity, their physiological effects depending largely upon the regions in which they terminate. The tracts which descend from the brain to the spinal cord arise partly in the midbrain (tractus tectospinalis) and partly from the medulla oblongata (tractus bulbospinalis), and here again there is little evidence of specificity of function, for these descending nervous impulses can do little more than modify the swimming reaction.

It is probable that the elaborate systems of sensorimotor connections which characterize the mammalian spinal cord have been derived from some such diagrammatically simple pattern as that which has just been described. As new and more complex movements are elaborated, particular chains of neurones become set apart for each specific reaction and isolated from the general nervous matrix which serves the simpler total reactions (see Herrick and Coghill, 1915).

THE CONDUCTION PATHWAYS OF THE SPINAL CORD.—*The Intrinsic Reflex Apparatus.*—For purposes of physiological analysis it is customary to hypothecate as the unit of behavior a simple reflex, whose mechanism in its most elementary form consists of a receptor, an afferent neurone, an efferent neurone, and the effector organ, with synaptic connection between the two neurones in the nerve center. Fig. 4578 illustrates the simplest possible mechanism of such a reflex in a segment of the spinal cord.

This schema is probably a pure abstraction, for no vertebrate spinal cord contains so simple a pattern of interneuronic connections, though this connection undoubtedly occurs as one component of more complex patterns. From the genetic standpoint, moreover, this direct connection of the afferent with the efferent neurone is, as we have seen above, the terminal rather than the initial stage in the elaboration of the spinal reflex apparatus.

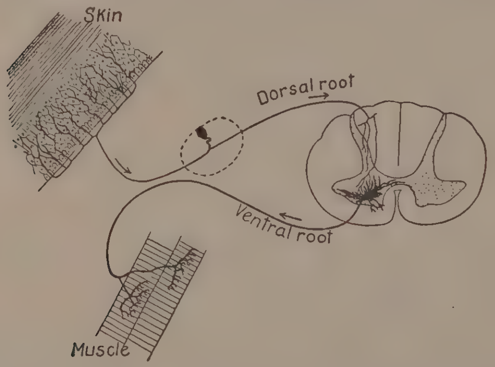

FIG. 4578.—Diagram Illustrating the Simplest Spinal Reflex Arc Consisting of Two Neurones, a Sensory Neurone Connected with the Skin and a Motor Neurone Connected with a Muscle. Physiological connection between the two neurones is effected within the spinal cord. (Modified from Van Gehuchten.)

The composition of a typical segmental spinal nerve is illustrated diagrammatically in Fig. 4579. The afferent fibers enter by the dorsal root and are of two sorts, somatic and visceral. The visceral fibers come in from the sympathetic nervous system. Their central connections are not well understood; they probably terminate, at least in part, in the intermediate zone of the gray matter. The somatic afferent fibers include both exteroceptive and proprioceptive systems (cf. the article, *End-organs, Nervous*).

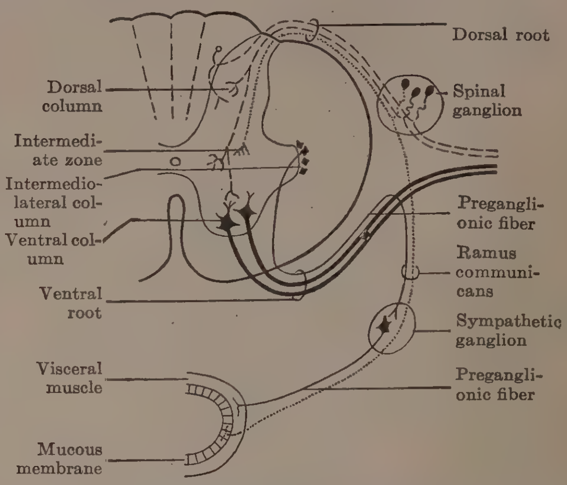

FIG. 4579.—Diagram Illustrating the Composition of a Typical Spinal Nerve in the Thoracic Region. The somatic sensory system is indicated by broken lines, the visceral sensory by dotted lines, the somatic efferent by heavy continuous lines, the visceral efferent (preganglionic fibers) by lighter continuous lines.

The efferent fibers leave the spinal cord generally in the ventral roots. In birds and some other vertebrates there is anatomical evidence that efferent fibers in small numbers leave by the dorsal roots also (Fig. 4572). The presence of such fibers in mammals is in controversy and their functions are unknown; probably they are of visceral type. The efferent fibers of the ventral roots are of two sorts, somatic and visceral, the former arising from cells of the ventral gray column and the latter from cells of

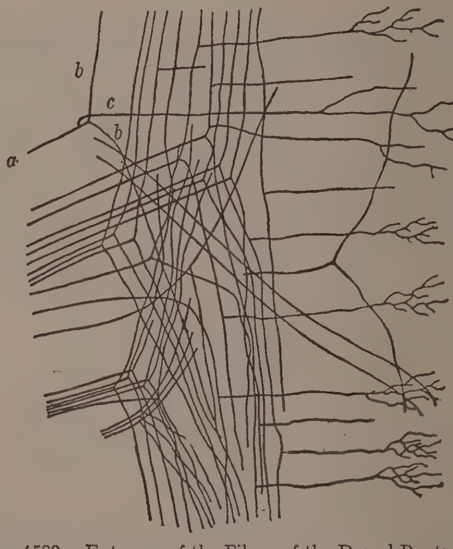

FIG. 4580.—Entrance of the Fibers of the Dorsal Roots into the Dorsal Funiculus of the Spinal Cord of an Embryo Calf. (After A. van Gehuchten, "Anatomie du système nerveux de l'homme," Louv., 2ed., 1897, p. 302, Fig. 205.) A stem fiber, *a*, is seen dividing into two branches, *b*, *b*, the ascending and descending limbs of bifurcation. From the stem fiber, *a*, a collateral, *c*, is seen to arise. A number of collaterals arising from the limbs of bifurcation of other fibers are illustrated.

the intermediolateral column. The visceral efferent fibers pass by way of the communicating branches into the sympathetic nervous system. They are the preganglionic fibers of Langley and always end in some sympathetic ganglion. Here there is a synapse and a second sympathetic neurone (postganglionic neurone) takes up the nervous impulse to transmit it to its appropriate end-organ. For further consideration of the functional analysis of the spinal nerves, see the article, *Cranial Nerves*.

The mode of entrance of the dorsal root fibers and their bifurcation into ascending and descending branches in the spinal cord is seen in Fig. 4580, and the various types of connection which these fibers make within the spinal cord are shown in Figs. 4581 and 4582.

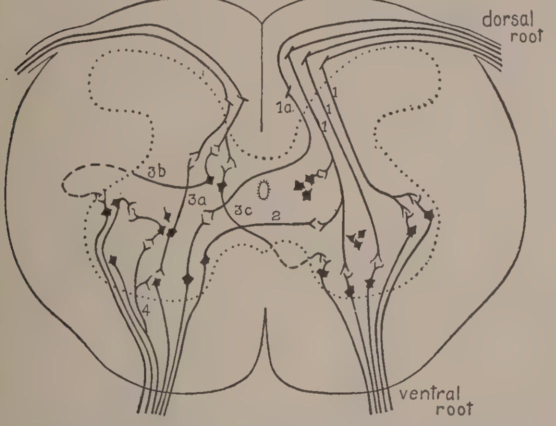

FIG. 4581.—Diagram of Some of the Types of Connection between the Sensory Fibers of the Dorsal Root and the Motor Fibers of the Ventral Root in the Spinal Cord of the Rabbit (chiefly after the researches of Philippson). The visceral connections are not included. 1. Collateral branches of the dorsal root fibers effect synaptic relations directly with dendrites of ventral column cells of the same or the opposite side. 2. Dendrites of ventral column cells may cross to the opposite side and here receive terminals of dorsal root fibers. 3. A correlation neurone may be intercalated between the two peripheral neurones in either of the first two cases. These neurones may have short axones for reflexes within a single segment (3*a*), or their axones may pass out into the white matter (fasciculus proprius) and extend for longer or shorter distances in either the ascending or the descending direction (or after branching in both directions) for connections with more remote motor centers of the same or the opposite side (3*b*, 3*c*). 4. The root fibers arising from the cells of the ventral column themselves may give off collateral branches which return to the gray matter and there arborize about other cells of the ventral column belonging to different functional groups or about correlation cells, thus facilitating the coordinated contraction of several distinct muscles in the performance of some complex reaction. The neurones of the dorsal column apparently do not play an important rôle as intercalary elements in the simpler spinal reflexes. The axones of these cells are for the most part directed upward, after decussating in the ventral commissure, and are chiefly concerned with the transmission of nervous impulses from the spinal cord to the higher correlation centers of the brain. (From Herrick's Introduction to Neurology.)

For the systems of intrinsic spinal reflexes collateral branchlets are given off from both the ascending and the descending branches of the dorsal root fibers. These collaterals may either connect directly with the neurones of the ventral gray columns at various levels, or more frequently one or more correlation neurones are intercalated between the peripheral sensory and motor neurones. Each of these types of connection is represented in a great variety of forms, some of which are illustrated in Fig. 4583.

The neurones of the dorsal column apparently do not play an important rôle as intercalary elements in the simpler spinal reflexes, these reactions being effected through the connections made directly with the ventral column or with the central groups of neurones (Fig. 4581, neurones 3*a*, 3*b*, 3*c*; Fig. 4583, *A* and *b*). The axones of the neurones of the dorsal column are apparently for the most part directed across the midplane and then upward in the spinal lemniscus; they are concerned chiefly with the transmission of nervous impulses from the spinal cord to the higher correlation centers of the brain.

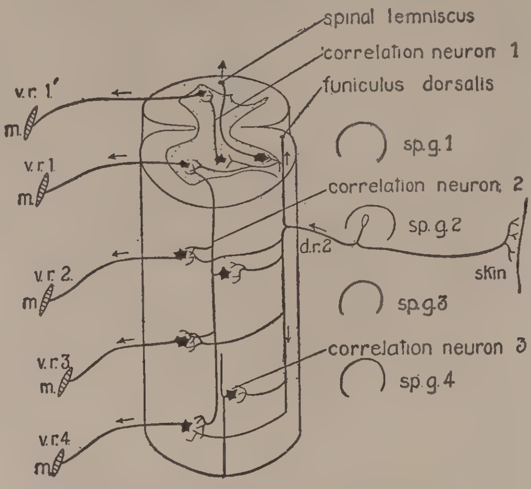

FIG. 4582.—Diagram of the Spinal Cord Reflex Apparatus. Some of the connections of a single afferent neurone from the skin (*d.r.*2) are indicated. *d.r.*2, Dorsal root from second spinal ganglion; *m*, muscles; *sp.g.*1 to *sp.g.*4, spinal ganglia; *v.r.*1' to *v.r.*4, ventral roots. (From Herrick's Introduction to Neurology.)

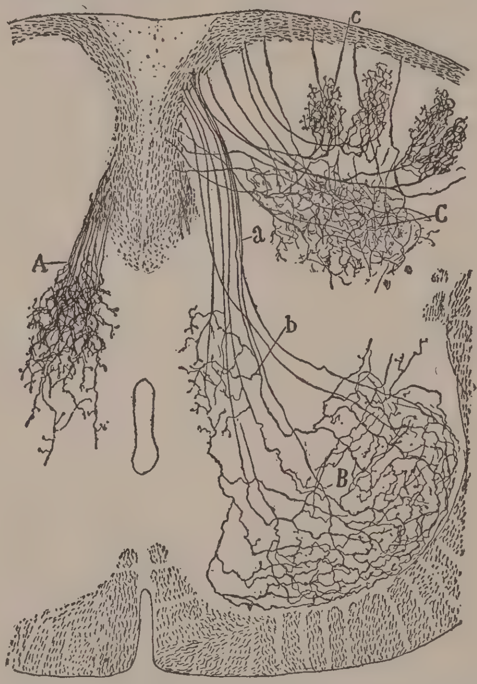

FIG. 4583.—Chief Sensory Collaterals in the New-born Rat (Golgi Stain). *A*, Collaterals for the intermediate gray nucleus; *B*, arborizations surrounding the motor nuclei; *C*, wide ramifications in the head of the posterior horn; a, sensory-motor fasciculus; b, collateral of one of the fibers destined for the intermediate gray nucleus; c, deep collaterals of the substance of Rolando. (After Cajal.)

The intrinsic spinal reflexes cannot be studied physiologically to advantage in any intact or normal higher animal because of the constant interference of the cerebral cortex and other higher centers. For such experiments the spinal cord of a laboratory animal is first severed in the lower cervical region, after which physiological experiments upon the isolated spinal cord can be made. Such an animal is the "spinal dog" upon which many important studies of the reflex types and their neurological mechanisms have been conducted.

In the dog there is a saddle-shaped area of skin over the shoulder (the "receptive field" of Fig. 4584), whose stimulation causes a characteristic scratch-reflex with the hind leg of the side stimulated. The nervous path involved is represented in Fig. 4584, B, *Rα-Pα-FC*. Reinforcement of the response is effected by the arrangement of neurones illustrated. Upon stimulation of two points ten centimeters apart within the saddle-shaped receptive field, the neurones *Rα* and *Rβ* are simultaneously excited. Through the propriospinal neurones *Pα*, *Pβ*, these impulses are discharged into a single efferent path, *FC*, and a scratch reflex will be evoked, even though the stimuli employed be so weak that neither stimulus alone will produce it. The mechanism of an antagonistic reflex can be seen in the same figure. If the receptive field on the left shoulder of a dog is stimulated, so as to produce the scratch reflex of the left leg (Fig. 4584, B, *Rα-Pα-FC*), and then while this reflex is in process a stimulus is applied to the right hind foot (*R*), the latter stimulus interferes with the former and inhibits the reflex. The stimulation of the right foot normally produces a totally different response (extension of the left knee). The two afferent impulses, accordingly, are in rivalry for the same final common path (*FC*) and one finally conquers the other. For the details of these and many other very instructive experiments the original accounts of Sherrington, as given in his Integrative Action of the Nervous System, should be consulted.

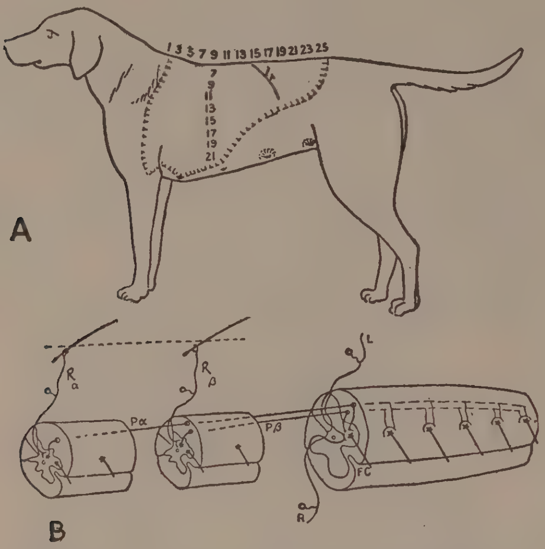

Fig. 4584.—*A*, The "Receptive Field" as Revealed after low Cervical Transection; a saddle-shaped area of dorsal skin, whence the scratch-reflex of the left hind limb can be worked; *lr* marks the position of the last rib. *B*, Diagram of the spinal area involved. *L*, receptive or afferent nerve-path from the left foot; *R*, receptive nerve-path from the opposite foot; *Rα*, *Rβ*, Receptive nerve-paths from hairs in the dorsal skin of the left side; *FC*, the final common path, in this case the motor neurone to a flexor muscle of the hip; *Pα*, *Pβ*, propriospinal neurones. (Sherrington.)

Philippson (1905) has studied the locomotor reflexes of the spinal dog in great detail and finds that in this animal the cord contains the complete mechanisms for these movements and that the movements of the trot and gallop can be executed when the feet are not in contact with the ground, *i.e.* by intrinsic mechanisms. When the lumbar segments are isolated from the remainder of the central nervous system, they are capable of coordinating the movements of the hind legs involved in the two types of locomotion, the trot and the gallop; and the cervical segments similarly can coordinate these movements of the fore legs.

The Connections between the Spinal Cord and the Brain.—In the analysis of the long conduction paths between the spinal cord and the brain it is helpful to keep constantly in mind the fundamental difference between the exteroceptive and the proprioceptive adjustments (see the article, *End-organs, Nervous*, vol. iv., p. 20). The reactions to exteroceptive stimuli are in general those by which the body is kept in adjustment with the changes occurring in the surrounding environment. The proprioceptive reactions are subsidiary to these, comprising in general the adjustments within the mechanisms of response themselves. The chief proprioceptive end-organs of the trunk and limbs are the neuromuscular receptors (in the muscle spindles), the nerve endings upon the tendons, and those of the joints, with some participation by cutaneous nerves. The neurones connected with these end-organs are constantly reporting back to the central nervous system the degree of contraction of the muscles, tension on the tendons, and amount of flexion of the joints. The return motor paths of these systems are the same as those from the exteroceptive receptors, for the function of the proprioceptors is mainly to exert a regulatory influence within the motor apparatus itself. This adjustment is for the most part effected unconsciously by the mechanisms of the spinal cord, brain stem, and cerebellum, though the cerebral cortex may also participate through the mediation of sensations of posture, equilibration and movements of the body and its members in space.

The somatic sensory impulses which enter the spinal cord by the dorsal roots, accordingly, are distributed with reference to four chief types of response: (1) for local reflexes within the spinal cord, (2) for cerebellar activities of the proprioceptive type (unconscious adjustments of equilibration and the orientation of the body in space), (3) for cerebral reactions of the proprioceptive type (conscious or unconscious adjustments of equilibration, posture, etc.), (4) for cerebral reactions of the exteroceptive type (conscious or unconscious adjustments in response to external stimulation). For each of these types of reaction there is a distinct system of neurones and conduction pathways in the spinal cord whose further analysis is our next task.

In the spinal ganglia and dorsal roots the fibers of these diverse functional systems are so intimately mingled as to have baffled analysis hitherto. This is incidental to the preservation of the primary segmental pattern more perfectly here than elsewhere in the nervous system. On the peripheral side of the ganglia the functional systems are separated and arranged in accordance with the physiological pattern of the surface of the body, and on the central side of the nerve roots there has been a rearrangement of the nerve fibers belonging to these same neurones in accordance with a different physiological principle, viz., the advantage of having all fibers serving the same physiological system of receptors (touch, temperature, pain, etc.) gathered together into a single tract regardless of the peripheral source of the stimulus.

Here again, we repeat that it is important to bear in mind the distinction between the exteroceptive and the proprioceptive systems and the fact that the central rearrangement of the peripheral nerve fibers, as soon as these enter the spinal cord and even before the first synapse is reached, is such as to segregate immediately all of the proprioceptive nervous impulses, from whatever source derived, from the exteroceptive impulses. After this primary separation has been effected, each of these great systems of conduction pathways is then further analyzed into separate tracts for fibers of diverse functions, such as temperature, touch, and pain sensibility.

We shall, therefore, find it convenient to consider the entire complex of somatic sensory pathways of the spinal nerves in four divisions which are topographically defined and which correspond with the changes in the functional patterns of the component nerve fibers as they are found at successive distances centralward from the peripheral receptors. These divisions are: (1) the peripheral division, carrying the nervous impulses up to the spinal ganglia; (2) the ganglia and dorsal roots of the spinal nerves; (3) the intraspinal division (including the central courses of the dorsal root fibers, the first synapse, and a part of the course of the fibers of the neurones of the second order); (4) the cerebral division.

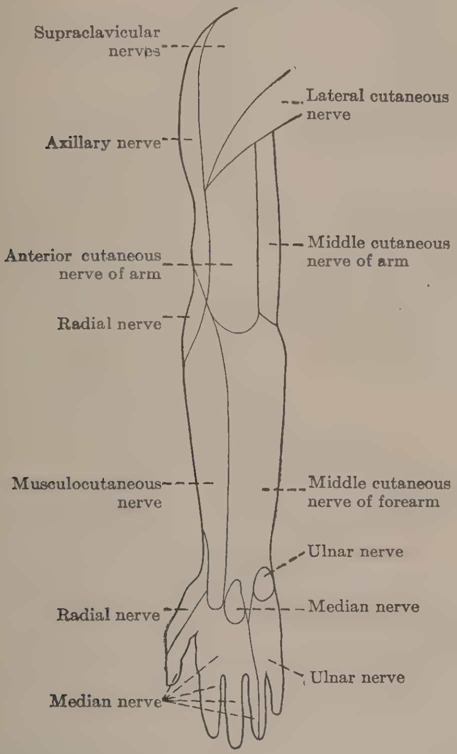

Fig. 4585.—A Diagram Illustrating the Areas of Skin Supplied by the Cutaneous Branches of the Nerves of the Arm and Hand.

The sensory fibers of the first division are distributed peripherally in two great groups of nerves, for deep sensibility and for cutaneous sensibility respectively. The deep, or muscular, branches of the spinal nerves are mixed in function, carrying motor fibers for the muscles and an equal or larger number of sensory fibers for muscle sense, tendon sense, and other forms of deep sensibility. The cutaneous branches of the spinal nerves serve chiefly the exteroceptive functions of touch, temperature, and pain. It should be borne in mind, however, that the deep sensory nerves participate to some extent in exteroceptive functions and the cutaneous nerves in proprioceptive functions, that is, the deep nerve endings are sensitive to external pressure and the cutaneous endings participate in the adjustments involving the sense of position, cutaneous localization, and the orientation of the body and its members in space.

In the region of the thorax the primitive segmental arrangement of the spinal nerves is preserved in the peripheral distribution of both the cutaneous and the muscular branches (see Plate LVI). The limbs in their embryological development grow out as lateral buds from the trunk, and in this process they carry with them a portion of each of the segments from which the limb buds arise. The result is that successive spinal nerve roots (from the fifth cervical to the second thoracic) innervate longitudinally arranged bands of skin on the arms. Thus, if the arms of the man shown in the plate last cited were held out in a horizontal position, the zonal distribution of spinal nerves as found in the trunk would be seen to extend outward into the arms with but slight changes in its pattern.

The nerves for the arms, however, do not pass directly from their roots to their distribution in the skin, as in the trunk, but they are first rearranged by a complicated series of anastomoses in the brachial plexus, so that the peripheral nerves as finally composed bear no simple relation to the segmental roots from which they arise. Fig. 4585 illustrates the areas of distribution of the chief cutaneous branches which supply the skin of the arm. The destruction of any one of these branches peripherally of the brachial plexus will result in anesthesia of the area of skin supplied by it, except for the margins of the area where there is an overlap of nerve endings from contiguous branches. Deep sensibility will be left intact so that, though the skin itself is anesthetic, strong pressure on the skin will be sensed and correctly localized by the deep nerve endings.

If, however, there is an injury to a peripheral sensory nerve for the arm at some point between the brachial plexus and the spinal cord, *i.e.* an injury to any spinal ganglion or root between the fifth cervical and the second thoracic segments, the anesthetic area on the skin of the arm will take a form similar to that shown on Plate LVI for the distribution area of that *root.* A study of the method of branching of the cutaneous nerves of the arm peripherally of the brachial plexus shows that no combination of peripheral injuries involving these branches could give the same pattern of anesthetic areas on the skin as would be produced by an injury to one or more spinal nerve roots. Furthermore, the destruction of any peripheral *cutaneous* branch would not disturb the underlying deep sensibility, so that strong pressure would still be sensed over the area in question, even though the skin is totally insensitive. On the other hand, the destruction of any dorsal nerve *root* which supplies the arm would result, not only in cutaneous anesthesia in accordance with the pattern shown in the plate, but also in some disturbance of deep sensibility also.

The nerves for the leg are similarly rearranged in the lumbosacral plexus, so that the cutaneous representation of the dorsal spinal roots does not bear any simple relation to the distribution areas of the peripheral cutaneous branches of the nerves for the leg.

Immediately upon entering the spinal cord the sensory fibers of the dorsal roots are again rearranged in accordance with a totally different principle, as will appear more fully beyond. These different rearrangements of the peripheral sensory nerve fibers before they enter the spinal cord and immediately within the cord must be recognized before we can continue our analysis of the peripheral sensory nerves. And since these differences have not always been taken account of in the clinical study of diseases of the spinal cord and its nerves, the published tables and diagrams of the peripheral representation of spinal cord segments are often confused and misleading (see Barker's Nervous System, Chapter 27, Head and Thompson in *Brain*, vol. xxix., 1906, p. 602, and Brouwer, Biologische Bedeutung der Dermatomerie, in Folia Neurobiologica, Bd. ix., 1915).

The entire series of cutaneous and deep sensations was formerly treated as a physiological and clinical unit under the name of "general sensibility," but of late the importance of a more critical analysis of this complex is appreciated. Since the disturbances of peripheral sensibility are the most commonly used clinical signs in the diagnosis of nervous diseases, these relations are of great practical importance. The analysis of the symptoms resulting from injuries to these conduction pathways will usually permit of a diagnosis of the site of the injury, whether it lies in the first or second division of the peripheral nerves or in the central nervous system.

Limiting our attention now to the first or peripheral division of the spinal nerves, we shall next summarize the results of the clinical analyses of Henry Head and his colleagues. These neurologists have classified the receptors of this division into three functional groups which serve respectively deep sensibility, protopathic sensibility, and epicritic sensibility. Deep sensibility is preserved after the destruction of all afferent cutaneous nerve fibers. It is chiefly concerned, as already stated, with the proprioceptive reflexes, *i.e.* with the unconscious coordination of muscular movement and the orientation of the body and its members in space; but some of its functions may also come into consciousness as exteroceptive sensations. By these nerves pressure can be recognized and discriminated and its point of application can be localized. The movements of muscles and joints can be recognized and pain results from an extreme pressure stimulus.

Protopathic sensibility, as defined by Head and his colleagues, is subjectively a general diffuse sensibility of a primitive form. Its sense organs are arranged in definite spots, and yet these sensations have no clear local reference or sign, that is, the spot stimulated cannot be accurately localized. There are separate spots for touch, heat, cold, and pain, these spots being generally associated with the hair bulbs. In fact, the hairs are the most important tactile organs of this system and the other sense qualities belonging here are intimately associated with the roots of the hairs. Either the protopathic or the epicritic sensations may be lost in some pathological cases without the abolition of the other or of the deep sensations. The protopathic group of sensations includes cutaneous pain, especially pricking, burning, and freezing pains, and also the extreme degrees of temperature discrimination, *i.e.* temperatures above 45° C. and below 20° C.

Epicritic sensibility is a more refined sort of discrimination and is regarded as a later evolutionary type. It includes light touch, on the hairless parts of the body particularly, and the discrimination of the intermediate degrees of temperature. Cutaneous localization and the discrimination of the distance between two points simultaneously stimulated (the "compass test") are functions of this system.

If a cutaneous nerve is severed, both the protopathic and the epicritic sensibility will be abolished, while deep sensibility is left intact. After some months the severed nerve fibers may regenerate and the sensory functions of the skin are gradually restored. In this regenerative process the protopathic functions reappear long in advance of the epicritic, a circumstance which permits of careful study of the physiological characteristics of these two systems. The results of these studies can best be summarized in the form of a table taken from Head and Thompson (1906).

Loss of *epicritic sensibility* abolishes—
Recognition of light touch over hairless parts or parts that have been shaved.
Cutaneous localization.
Discrimination of compass points.
Appreciation of differences in size, including the accurate discrimination of the head from the point of a pin apart from the pain of the prick (acuæsthesia).
Discrimination of intermediate degrees of temperature from about 25° C. to about 40° C.

Loss of *protopathic sensibility* abolishes—
Cutaneous pain, especially that produced by pricking, burning, or freezing, together with that of stimulation with a painful interrupted current. Over hair-clad parts, plucking the hairs ceases to be painful.
Sensations of heat from temperatures above about 45°C.
Sensations of cold from temperatures below 20° C.

After destruction of all cutaneous afferent fibers the part is still endowed with *deep sensibility.*
Pressure can still be recognized, and its gradual increase appreciated.
Pain is produced by excessive pressure (measured by the algometer).
Movements of muscles can be recognized.
The point of application of pressure can be localized.
The patient can recognize the extent and direction of movement produced passively in all the joints within the affected area.

This analysis was based in the first instance upon clinical data. In order to make further studies under the most favorable conditions, Dr. Head in the year 1903 secured the services of other surgeons and had an experimental operation performed on his own body (Rivers and Head, 1908), severing near the left elbow the superficial branch of the radial nerve for the forearm and the musculocutaneous (external cutaneous) nerve. After the operation a well-defined area of the forearm and hand was found to be insensitive to protopathic and epicritic sensibility, the area anesthetic to painful stimuli (prick with a pin) being not exactly coextensive with that devoid of tactile sensibility (Fig. 4586). All forms of deep sensibility were entirely unaffected. During a period of nearly five years following the operation the physiological and psychological symptoms of the affected cutaneous area were carefully studied, a thorough examination being made weekly during most of the period of repair. In this way Dr. Head was able to watch in his own person the steps in the successive appearance of the protopathic and the epicritic functions and to

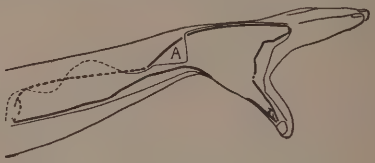

Fig. 4586.—Lateral View of Dr. Head's Left Hand One Month after the Operation which Severed the Superficial Branch of the Radial Nerve and the Musculocutaneous (External Cutaneous) Nerve near the Elbow. The area enclosed within the thin line was insensitive to epicritic tactile stimuli (light touch), and the area enclosed within the thick line was insensitive to painful and thermal stimuli also (loss of both epicritic and protopathic cutaneous sensibility). Deep sensibility was unaltered in the entire region. The triangular area marked *A* was insensitive to cutaneous pain, to cold, and to extreme degrees of heat (above 50° C.), but was sensitive to delicate stimulation with cotton wool and to moderate degrees of warmth. This was interpreted to mean that the epicritic sensibility was intact though the protopathic sensibility was lost. Where the boundaries of the area of loss of sensibility were ill-defined the limiting lines are broken.

determine the part which each plays in the complex commonly called "general sensibility."

The history of the process of repair and return of function in this case may be briefly summarized as follows:

Forty-three days after the operation the regeneration of the proprioceptive nerves had begun to be apparent and the area of insensitiveness to cutaneous pain (prick) had begun to diminish.

Eighty-six days after the operation the whole forearm responded to prick and the back of the hand was becoming rapidly sensitive to this stimulus. Cold was not appreciated except in the terminal joint of the thumb, and 50° C. gave no sensation of heat.

One hundred and thirty-seven days after the operation the whole forearm had become sensitive to cold.

One hundred and seventy-three days after the operation the whole back of the hand had become sensitive to prick and in a less degree to cold. Sensibility to heat appeared shortly before this date and rapidly improved.

Three hundred and sixty-five days after the operation the first sensibility to light (epicritic) touch appeared and the protopathic sensibility had still further improved and soon became normal.

Four hundred and twenty-eight days after the operation epicritic sensibility to temperature returned on the forearm.

Five hundred and sixty-seven days after the operation epicritic sensibility had returned over the greater part of the affected area, though a small part has remained permanently in the protopathic condition.

Trotter and Davies (1909) extended the observations which Head made upon his own person by similar operations made upon themselves in which in all seven cutaneous nerves were severed and the processes of repair very carefully studied. Some of their conclusions are as follows:

In each case the area of skin supplied by the nerve showed in consequence of the operation defects in seven distinct functions: four sensory, namely, sensibility to touch, cold, heat, pain; and three motor, namely, vasomotor, pilomotor, sudomotor.

In each case the sensory changes showed a central area of profound loss; an area of moderate extent surrounding this of partial loss; and a large area in which a qualitative change could be detected. The loss of motor function showed a central area of profound loss and a surrounding area of partial loss. The seven areas corresponded on the whole fairly closely but no two of them coincided absolutely.

During a certain period following the nerve section, from about the second to the sixth week, hyperalgesia may appear. The characters of it point to its being a complication due to the presence of an irritative change rather than to its being due to any kind of sensory loss.

Sensibility to touch is subserved by a nervous mechanism distinct from that of sensibility to pressure; the former occurs in the skin only, the latter in structures deep to the skin. It is probable, however, that the skin possesses some sensibility to pressure. A touch sensation is introspectively quite distinct from a pressure sensation. The touch sensation is intimately associated with movement.

Recovery of all the functions which are dependent upon regeneration begins about the same time. The rate at which the various returning functions spread over the area is about equal, but the rate at which they progress toward normal acuity is not so.

Sensations derived from a recovering area show a remarkable qualitative peculiarity. Cold, pain and the pain element of heat are intensified, but touch is little changed, though more difficult to elicit. A large number of sensations elicited from a recovering area are referred to distant parts of the area or to the point of the nerve section. The referred sensation may be felt alone or combined with a local sensation. Peripheral reference is the earliest phenomenon of recovery and the last sign of abnormality.

It appears that in general (though with some notable exceptions) Trotter and Davies found the facts presented by their experiments to be very similar to those of Head and his colleagues, with, however, a considerable refinement of the methods of research and a corresponding enlargement of the actual findings. The interpretation of their data lead Trotter and Davies to conclusions in several respects widely at variance from those of Head. Some of these differences are suggested in the preceding summary.

As indicated earlier in this article, Head arranges cutaneous sensations in two groups called protopathic and epicritic and he is inclined to believe that each sense quality in each of these groups is served by nerve fibers distinct from the others. Trotter and Davies do not interpret their data as supporting the separate individuality of the protopathic and the epicritic types of sensibility, but seem more inclined to regard these types as physiological phases of a single group of sensations.

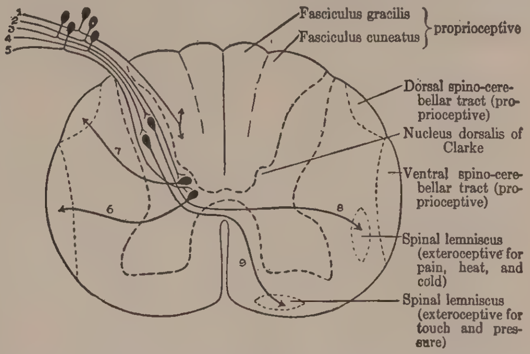
1
2
3
4
5
Fasciculus gracilis
Fasciculus cuneatus
proprioceptive
Dorsal spino-cerebellar tract (proprioceptive)
Nucleus dorsalis of Clarke
Ventral spino-cerebellar tract (proprioceptive)
Spinal lemniscus (exteroceptive for pain, heat, and cold)
Spinal lemniscus (exteroceptive for touch and pressure)
6
7
8
9

Fig. 4587.—Diagram to Illustrate the Terminations within the Spinal Cord of Some of the Types of Somatic Sensory Fibers and Their Secondary Paths. The central connections of root fibers 1, 2, and 5 provide for proprioceptive responses; those of fibers 3 and 4 for exteroceptive responses. Root fiber 1 terminates in the nucleus of the fasciculus cuneatus of the same side at the upper end of the spinal cord and conveys impulses of muscular sensibility, sense of passive positions and movement and of spatial discrimination. Root fiber 2 terminates in the nucleus dorsalis of Clarke (Clarke's column) and root fiber 5 in the same nucleus or adjacent parts of the gray substance. These fibers call forth unconscious cerebellar activity underlying the coordination and reflex tone of the muscles. Root fibers 3 and 4 terminate in the dorsal gray column and convey exteroceptive impulses. Fiber 3 typifies all fibers which carry sensibility of pain, heat, and cold; fiber 4 those which carry sensibility of touch and pressure. (From Herrick's Introduction to Neurology.)

It has been pointed out that the type of functional distribution of nerve fibers found in the first division of the peripheral nerves is replaced in the second division by a purely segmental arrangement in which all functional systems of fibers are mingled in the spinal nerve roots. We must next consider the further rearrangement of these functional systems of fibers which takes place within the spinal cord (our third division).

The guiding principles of this rearrangement have already been briefly stated. In the first place, the proprioceptive and the exteroceptive elements of the dorsal root complex are separated and then each of these groups is further analyzed into separate conduction pathways for special systems of sensory fibers. From all systems of peripheral root fibers connections are effected for local reflexes within the spinal cord. Some illustrations of the mechanisms of these intrinsic spinal reflexes were presented in the preceding section. The ascending pathways from the cord to the brain are analyzed as follows (Fig. 4587).

The exteroceptive systems (touch, temperature, and pain) form the spinal lemniscus to the medulla oblongata, midbrain, and thalamus, the last-mentioned fibers being the tractus spinothalamicus. The proprioceptive systems are distributed partly to the cerebellum through the spinocerebellar tracts and partly to the medulla oblongata, midbrain, and thalamus through the dorsal funiculus of the cord (fasciculus gracilis and cuneatus) and medial lemniscus of the brain. The proprioceptive pathways will first be discussed.

The main ascending *proprioceptive path* is composed of the root fibers which form the dorsal funiculi of the cord. It will be recalled that immediately upon entering the spinal cord the dorsal root fibers divide into ascending and descending branches and that collaterals leave both of the branches to terminate in synaptic relations with the cells of the gray substance of the cord. Many of these collateral terminals provide for intrinsic spinal reflexes, but the main ascending branches of the proprioceptive neurones continue upward in the dorsal funiculus of the same side of the cord to its upper end (Fig. 4591). Here they terminate in the nuclei of the fasciculus gracilis and fasciculus cuneatus, which are masses of gray matter lying at the boundary beween the spinal cord and medulla oblongata. The dendrites of the neurones of these nuclei effect synaptic connections with these terminals and their axones form the medial lemniscus of the brain, or fillet. The fibers of the medial lemniscus decussate immediately after leaving the nuclei of the dorsal funiculus, thus forming the decussation of the lemniscus. The longest fibers of the medial lemniscus system reach the thalamus of the opposite side and after a synapse here their nervous impulses may be carried forward into the cerebral cortex through the sensory thalamocortical radiations.

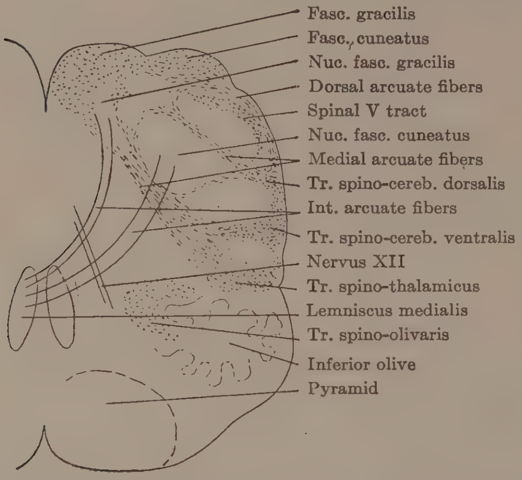

Fig. 4588.—Transverse Section through the Lowest Part of the Human Medulla Oblongata, showing by Marchi's method the degenerations resulting from a tumor in the second lumbar segment, and illustrating the tractus spinocerebellaris posterior of Goldstein (marked dorsal and medial arcuate fibers on the figure) passing from the fasciculus gracilis and cuneatus to the spinocerebellar tracts. (Based on the researches of Goldstein, 1910.)

The cortical proprioceptive pathway in its simplest form may consist of only three neurones: (1) A peripheral spinal neurone, whose cell body lies in some spinal ganglion, whose peripheral fiber terminates in some organ of musculotendinous sensibility or similar receptor, and whose axone terminates at the upper end of the cord in the nucleus of the fasciculus gracilis or cuneatus of the same side. (2) The body of the second neurone lies in one of the nuclei last mentioned (marked nucleus of dorsal funiculus on Fig. 4591) and its axone enters the medial lemniscus and terminates in the thalamus of the opposite side. The neurone of the third order lies in the thalamus and sends its axone through the

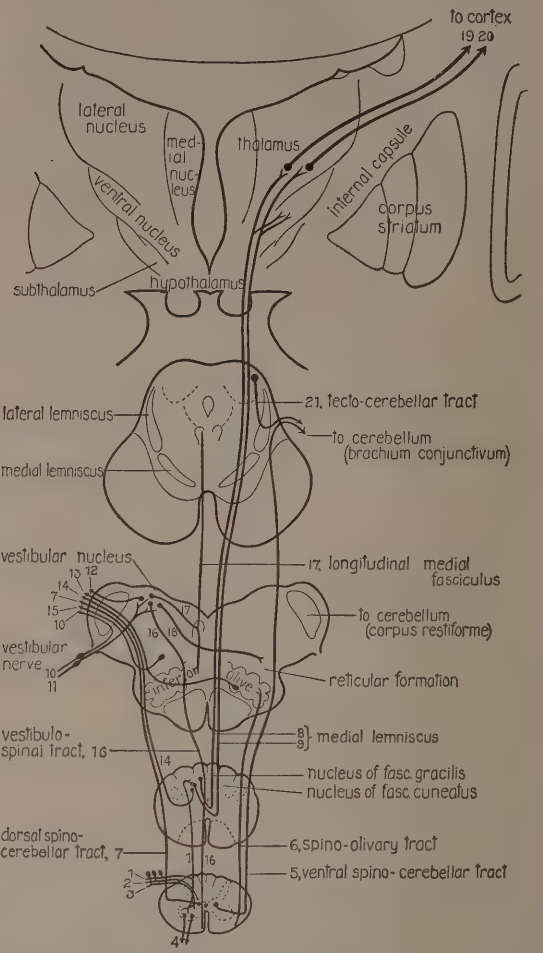

Fig. 4589.—Diagram of the Chief Proprioceptive Conduction Pathways Contained within the Spinal Cord and Brain Stem. The mesencephalic root of the trigeminal nerve is omitted and not all of the cerebellar connections are indicated. The connection to the cerebellum from the nuclei of the fasciculi gracilis and cuneatus (neurone 14) is controverted, but it is well established that similar connections are effected immediately below this level from the dorsal funiculus of the cord (cf. Fig. 4588). The figure illustrates cross-sections of the central nervous system in the lower cervical region of the spinal cord, at the level where the cord passes over into the medulla oblongata, at the level of the roots of the VIII cranial nerve, through the inferior colliculus, and through the thalamus. 1. Peripheral neurone entering the dorsal funiculus and also effecting intrinsic spinal reflex connections. 2. Peripheral neurone entering the nucleus dorsalis of Clarke. 3. Peripheral neurone effecting connections with the intrinsic correlation neurones of the spinal cord. 4. Peripheral motor neurones of spinal nerve. 5. Ventral spinocerebellar tract. 6. Spinoolivary tract. 7. Dorsal spinocerebellar tract. 8, 9. Medial lemniscus. 10. Vestibular root fiber passing directly into the cerebellum. 11. Vestibular root fiber entering the vestibular nucleus. 12. Vestibulocerebellar tract. 13. Olivocerebellar tract. 14. Path from the dorsal funiculus (or its nuclei) to the cerebellum. 15. Path from the reticular formation to the cerebellum. 16. Vestibulospinal tract. 17. Path from the vestibular nucleus to the fasciculus longitudinalis medialis. 18. Path from the vestibular nucleus to the reticular formation. 19, 20. Thalamic radiations to the cerebral cortex. 21. Tectocerebellar tract. (From Herrick's Introduction to Neurology.)

internal capsule to the somesthetic area of the cerebral cortex.

The reflex connections of the proprioceptive type for motor coordination in the spinal cord, medulla oblongata and midbrain are undoubtedly very primitive. But comparative anatomy suggests that the thalamic and cortical connections of the medial lemniscus system are phylogenetically more recent, and clinical evidence shows that these later connections are concerned with the conscious adjustments of the positions and orientation in space of the body and its members and with various types of spatial discrimination, rather than with simple reflexes. The cerebellum, on the other hand, was developed very early in vertebrate evolution as the general overlord of the proprioceptive system.

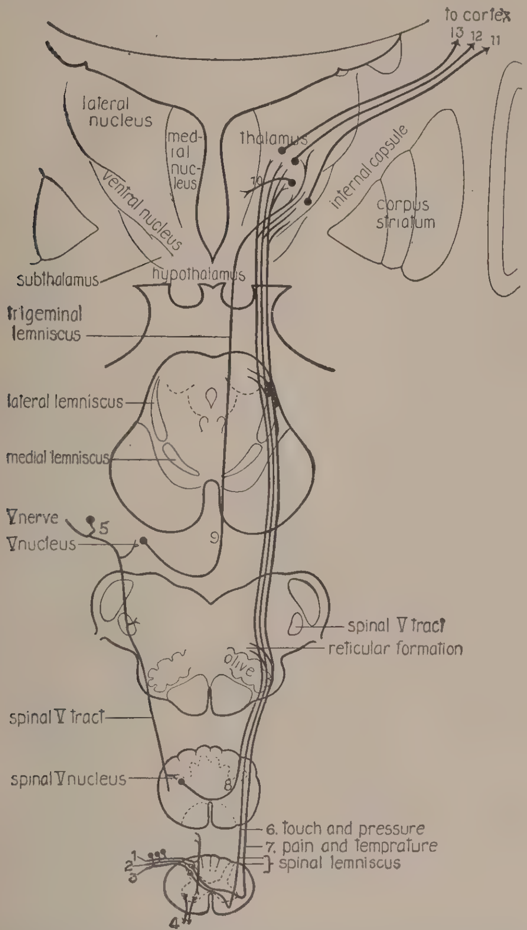

Fig. 4590.—Diagram of the Exteroceptive Conduction Pathways Contained within the Spinal Cord and Brain Stem. The figure illustrates cross-sections of the central nervous system in the lower cervical region of the spinal cord, at the level where the cord passes over into the medulla oblongata, at the level of the roots of the VIII cranial nerve, through the inferior colliculus, and through the thalamus. 1. Connections of peripheral neurone of touch, temperature, or pain for intrinsic spinal reflexes. 2. Peripheral neurone of pain or temperature. 3. Peripheral neurone of touch and pressure. 4. Peripheral motor neurones of spinal nerve. 5. Peripheral cutaneous neurone of trigeminal nerve. 6. Secondary neurone of touch and pressure in spinal lemniscus. 7. Secondary neurone of pain or temperature in spinal lemniscus. 8. Secondary neurone from lower part of spinal V nucleus entering the spinal lemniscus. 9. Secondary neurone from chief sensory V nucleus entering the trigeminal lemniscus. 10. Intrinsic correlation neurone of thalamus for thalamic reflexes. 11, 12, 13. Thalamocortical radiations to the postcentral gyrus. (From Herrick's Introduction to Neurology.)

There are three spinocerebellar pathways belonging to this system, (1) the ventral spinocerebellar tract, (2) the dorsal spinocerebellar tract, (3) a cerebellar connection from the dorsal funiculus (Figs. 4587, 4589 and 4592). The peripheral proprioceptive nervous impulses destined for the first and second of these tracts enter by way of the dorsal roots and near their level of entrance are discharged into the nucleus dorsalis of Clarke. After a synapse here, the axones of the neurones of the second order pass to the lateral surface of the cord and then upward to the cerebellum. The fibers of the dorsal cerebellar tract arise from the nucleus dorsalis and pass upward without decussation; this path is therefore often called the direct cerebellar tract (also called Flechsig's tract and, incorrectly, in the BNA tables the fasciculus cerebellospinalis). The fibers of the ventral cerebellar tract (part of Gowers' tract and of the fasciculus anterolateralis superficialis of the BNA), according to the older descriptions, arise from neurones of the intermediate region under the dorsal gray column, chiefly in the lower levels of the cord, and most of them cross to the opposite side of the cord before turning upward. But the recent experiments of A. N. Bruce have convinced him that all of the fibers of this tract have the same origin as do those of the dorsal tract, viz., from the nucleus dorsalis of the same side.

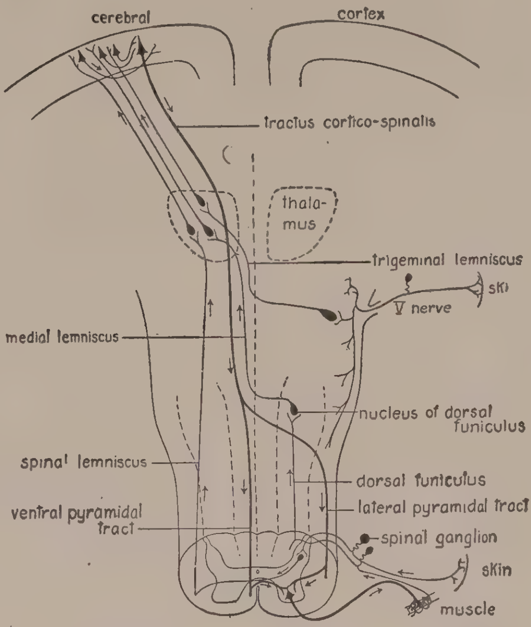

Fig. 4591.—Diagram of the chief Connections between the Spinal Cord and the Cerebral Cortex. The spinal lemniscus complex carries the ascending exteroceptive systems (touch, temperature, and pain); the dorsal funiculus and medial lemniscus complex carries chiefly ascending proprioceptive systems (a nerve of muscle sense is the only member of this group included in the drawing). The diagram also includes the sensory path from the skin of the head to the cerebral cortex through the nervus trigeminus and the trigeminal lemniscus. The pyramidal tract (tractus corticospinalis) is the common descending motor path for both exteroceptive and proprioceptive nervous impulses from the cerebral cortex. (From Herrick's Introduction to Neurology.)

The third group of spinocerebellar fibers, from the dorsal funiculus, is much less perfectly known than are the other two. Some neurologists deny their existence altogether. Goldstein (1910) has recently shown that some fibers from both the fasciculus gracilis and the fasciculus cuneatus pass lateralward in the upper levels of the spinal cord and lower part of the oblongata as dorsal external and medial arcuate fibers (Fig. 4588) to enter the dorsal and ventral spino-cerebellar tracts, and thus reach the cerebellum of the same side. He terms this the tractus spinocerebellaris posterior. It is not known whether these are root fibers or fibers of the second order. Fibers have often been described as arising in the nucleus of the fasciculus gracilis and fasciculus cuneatus to enter the cerebellum through the restiform body, but the existence of these fibers is very doubtful. The chief proprioceptive pathways are assembled in Fig. 4589.

Turning now to the *exteroceptive fibers* of the spinal nerves serving the sensations of touch, temperature and pain, attention should again be called to the fact that these fibers are derived chiefly from the cutaneous branches of the spinal nerves, though some come also from the deep branches and convey the sensory impulses excited by deep pressure and deep pain. Unlike many of the proprioceptive fibers which run upward in the dorsal funiculus to its upper end before terminating, these exteroceptive fibers all terminate in the gray substance within a very few segments of their points of entrance. The neurones of the second order lie in the dorsal gray column and their axones immediately cross to the opposite side of the cord where they ascend in one of the tracts which make up the spinal lemniscus, or tractus spinothalamicus (Figs. 4587, 4590, 4591, and 4592).

Furthermore, it is important to note that as the fibers of the spinal lemniscus decussate, a few at a time throughout the length of the cord, they are segregated functionally and all fibers concerned with sensations of touch and pressure enter the ventral funiculus (ventral spinothalamic tract), while those concerned with pain and temperature enter the lateral funiculus (lateral spinothalamic tract, Figs. 4587 and 4592). And in the lateral funiculus the fibers conveying impulses of pain are more or less separated from those for heat and cold. From this it follows that small circumscribed injuries in the white substance of the spinal cord may destroy all sensibility to pressure in a part of the body below the site of the injury, without any disturbance whatever of pain or temperature sensibility, or of pain or temperature without any involvement of the other sense qualities.

Some peculiar combinations of symptoms arise from the fact that, whereas the ascending proprioceptive impulses (so far as these are consciously perceived) pass up in the dorsal funiculus of the *same* side for the entire length of the cord, the impulses of the exteroceptive impulses, within a few segments of their point of entrance into the cord, are transferred to the *opposite* side to ascend in the spinal lemniscus tracts. From this it follows that a localized central injury involving the dorsal gray column and dorsal funiculus of one side only will cut off all ascending proprioceptive impulses which pass through the dorsal funiculus from lower levels on the same side of the body as the lesion, and at the same time will abolish both proprioceptive and exteroceptive functions in a circumscribed region of the same side of the body whose exteroceptive neurones of the first order discharge into the injured part of the dorsal gray column.

The dorsal funiculi of the spinal cord have until recently been regarded as the chief ascending pathway for all forms of sensibility, and much of the clinical practice now in vogue is based upon this assumption. But evidently such an assumption is untenable. The dorsal funiculi seem to be concerned chiefly with the proprioceptive group of reactions. These may be unconscious reflexes of motor coordination and the maintenance of equilibrium, or they may come into consciousness as sensations of position and orientation of the body and its parts and of spatial discrimination. Purely exteroceptive stimuli, whether transmitted by the deep nerves or by the cutaneous nerves, may be carried for a few segments in the dorsal funiculi; but they are soon filtered off into the gray matter of the dorsal column, and after a synapse here they are sorted into functionally distinct tracts on the opposite side of the cord. The tactile elements of the mixed peripheral root fibers entering the dorsal funiculus are drawn off later than are the elements for thermal and painful sensibility; and some of the components commonly reckoned with cutaneous exteroceptive sensibility remain in the dorsal funiculus for its entire length. These are chiefly two-point discrimination, and discrimination of size, shape, form, and texture of surfaces. These all involve a comparison and discrimination in consciousness of spatial factors and are therefore bound up with those fibers which serve the proprioceptive reflexes, which are unconscious spatial adjustments.

In addition to the ascending systems between the spinal cord and the brain already considered, there are others which serve purely reflex functions of various sorts, such as the tractus spino-olivaris of Goldstein (Fig. 4592) between the cord and the inferior olive of the medulla oblongata. The descending tracts from the brain to the cord (Figs. 4591 and 4592) include the great pyramidal tracts (tractus corticospinalis) and various reflex pathways from the brain stem, such as the tractus tectospinalis and the tractus rubrospinalis from the midbrain, and the tractus vestibulospinalis from the nuclei of the VIII cranial nerve.

We cannot include here a full discussion of the conduction pathways of the spinal cord. In Fig. 4592 the locations of some of the more important tracts of the cervical cord are diagrammatically indicated. A list of these and some other tracts follows. The names here employed in some cases differ from those of the official list by the German Anatomical Society, the BNA terms being here italicized.

Ascending Tracts.—*Fasciculus gracilis* (column of Goll) and *fasciculus cuneatus* (column of Burdach). These are mixed bundles which in the aggregate make up the greater part of the dorsal funiculus (old term, posterior columns). They are made up chiefly of the ascending branches of dorsal root fibers (Fig. 4582), those in the gracilis from the sacral, lumbar, and lower thoracic nerves (Fig. 4592, *S*, *L*, *T* 5–12) and those in the cuneatus from the upper thoracic and cervical nerves (*T* 1–4, *C*) as indicated in Fig. 4592. These fasciculi terminate respectively in the nuclei of the fasciculus gracilis (clava) and cuneatus (tuberculum cuneatum) at the lower end of the medulla oblongata and conduct chiefly impulses of the proprioceptive reflexes and those concerned with sensations of posture, spatial discrimination and the coordination of movements of precision.

Fasciculus dorsolateralis (tract of Lissauer, Lissauer's zone), made up chiefly of unmyelinated fibers from the dorsal roots, together with myelinated and unmyelinated correlation fibers of the fasciculus proprius system.

Tractus spinocerebellaris dorsalis (*fasciculus cerebello-spinalis*, direct cerebellar tract, Flechsig's tract). These fibers arise from the neurones of the *nucleus dorsalis* (Clarke's column of gray matter between the dorsal and ventral gray columns in the thoracic region) of the same side and enter the cerebellum by way of its inferior peduncle (*corpus restiforme*).

Tractus spinocerebellaris ventralis (partof Gowers' tract, or the *fasciculus anterolateralis superficialis* of the BNA). These fibers also arise from the nucleus dorsalis of the same side (A. N. Bruce) in the lower levels of the spinal cord and enter the cerebellum by way of its superior peduncle (*brachium conjunctivum*).

The spinal lemniscus. Under this name are included several tracts to the midbrain and thalamus. These fibers arise from neurones of the dorsal gray column, cross in the ventral commissure, and ascend in the lateral and ventral funiculi of the opposite side, partly superficially mingled with those of the ventral spinocerebellar tract and partly deeper in the fasciculus proprius. This system of fibers includes a tractus spinotectalis to the roof (tectum) of the midbrain and a tractus spinothalamicus to the ventral and lateral nuclei of the thalamus. The deeper fibers of the latter tract are arranged in two groups, the tractus spinothalamicus lateralis for sensory impulses of temperature and pain, and the tractus spinothalamicus ventralis for sensory impulses of touch and pressure.

Tractus spino-olivaris, fibers arising from the entire length of the spinal cord and terminating in the inferior olive (Goldstein).

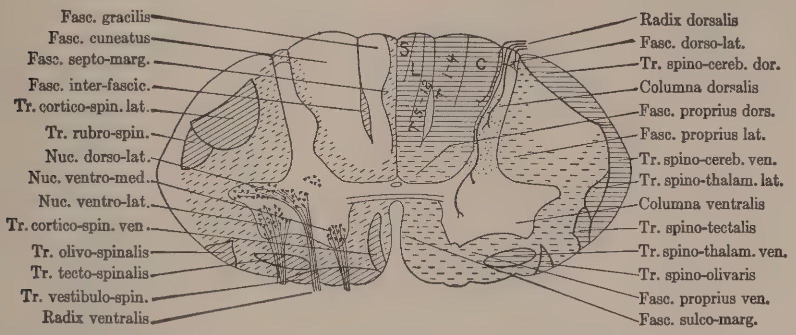

FIG. 4592.—Diagram of a Cross-section through the Human Spinal Cord at the Level of the Fifth Cervical Nerve, to illustrate the arrangement of the fiber tracts in the white matter and of the nerve cells in the gray matter of the ventral column. On the right side the area occupied by the dorsal gray column (posterior horn) is stippled; on the left side some of the groups of cells of the ventral gray column (anterior horn) are indicated. In the white matter the outlines of some of the more important tracts are schematically indicated, ascending fibers on the right side and descending fibers on the left. The same area of white matter is in some cases shaded on both sides of the figure. This indicates that ascending and descending fibers are mingled in these regions. It should be emphasized that none of the tracts are so sharply delimited as here figured, but that their boundaries are indefinite with much mingling of fibers of diverse sorts in the same area of the cross-section. (From Herrick's Introduction to Neurology.)

DESCENDING TRACTS.—Tractus corticospinalis (*fasciculus cerebro-spinalis*, pyramidal tract). This system of fibers conducts voluntary motor impulses from the precentral gyrus of the cerebral cortex to the motor centers of the spinal cord. It divides at the upper end of the spinal cord into two tracts, the larger division immediately crossing through the decussation of the pyramids to the opposite side of the spinal cord, where it becomes the tractus corticospinalis lateralis (*fasciculus cerebrospinalis lateralis*, lateral or crossed pyramidal tract). A smaller number of these fibers pass downward into the spinal cord from the medulla oblongata without decussation to form the tractus cortico-spinalis ventralis (*fasciculus cerebrospinalis anterior*, direct pyramidal tract, column of Türck). These fibers cross in the ventral commissure a few at a time throughout the upper levels of the cord, and finally terminate in relation with the motor neurones of the opposite side. Both parts of the pyramidal tract, therefore, decussate before their fibers terminate.

Tractus thalamo-spinalis. Fibers from the thalamus to the spinal cord were described by Meynert in the fasciculus proprius ventralis and by von Bechterew in the fasciculus proprius lateralis. This connection is denied by others for mammals. There is certainly an important descending system from the thalamus, but whether these fibers reach as far down as the spinal cord must be regarded as unsettled.

Tractus rubrospinalis (tract of Monakow). From the nucleus ruber of the midbrain to the lateral funiculus of the cord for thalamic and cerebellar reflexes.

Tractus tectospinalis (predorsal bundle, tract of Löwenthal). These fibers arise from the roof (tectum) of the midbrain and enter the ventral funiculus of the cord. Part of the fibers of this system pass downward without decussation; others, while still within the midbrain, cross to the opposite side under the aqueduct of Sylvius, forming the dorsal decussation of the tegmentum or fountain decussation of Meynert.

Tractus vestibulospinalis, from the primary centers of the vestibular nerve in the medulla oblongata to the spinal cord, for equilibratory reflexes.

The two tracts last mentioned, together with several others, compose the *fasciculus marginalis ventralis*.

Tractus cerebellospinalis. There has been much controversy regarding the existence of a direct pathway from the cerebellum to the spinal cord without interruption in the brain stem. It seems well established that fibers arising from neurones of the dentate nucleus pass out through the brachium conjunctivum and enter the ventrolateral region of the spinal cord (fasciculus marginalis ventralis).

Tractus olivospinalis (Helwig's bundle, tractus triangularis). These fibers descend from the inferior olive of the medulla oblongata to the lower cervical or upper thoracic segments of the spinal cord in the lateral funiculus.

Fasciculus longitudinalis medialis (posterior longitudinal bundle). Fibers of this important system of the brain stem are known to enter the fasciculus sulcomarginalis of the ventral funiculus of the cord.

Tractus bulbospinalis. This general term may be applied to fibers other than those described above, which descend from the medulla oblongata to the lateral and ventral fasciculus proprius of the cord. Fibers of this sort arise from the motor tegmentum of the medulla oblongata, and others less certainly established have been described as arising in the nuclei pontis and nuclei arcuati.

THE FASCICULUS PROPRIUS.—The fasciculus proprius system of fibers (also called ground bundles and fundamental columns) comprises chiefly short ascending and descending fibers arising from neurones of the spinal gray matter, for intrinsic spinal reflexes. In general these fibers border the gray pattern, but in the dorsal funiculus some are aggregated in the tractus septomarginalis and the fasciculus interfascicularis (comma tract, tract of Schultze), these two tracts also containing descending branches of the dorsal root fibers. Some fibers of the fasciculus proprius ventralis lie adjacent to the ventral fissure and are termed the fasciculus sulcomarginalis, these fibers forming the direct continuation into the cord of the fasciculus longitudinalis medialis (posterior longitudinal bundle) of the brain.

NOTE.—In the preparation of this article free use has been made of Dr. L. F. Barker's article, *Spinal Cord*, in the second edition of this Handbook.

C. Judson Herrick.

Literature.

Adamkiewicz, A.: Die Blutgefässe des menschlichen Rückenmarks. Sitzungb. d. k. Akad. d. Wissensch., Math.-Natur. Cl., 3 Abt., Wien, Bd. lxxxiv., 1882, SS. 469–502.

Barker, L. F.: The Nervous System and Its Constituent Neurones, New York, 1901.

Bartlemez, G. W.: Mauthner's Cell and the Nucleus Motorius Tegmenti. Jour. Comp. Neur., vol. xxv., 1915, pp. 87–128.

Borchert, M.: Experimentelle Untersuchungen an den Hintersträngen des Rückenmarks. Arch. f. (Anat. und) Physiol., 1902.

Brouwer, B.: Die biologische Bedeutung der Dermatomerie. Beitrag zur Kenntnis der Segmentalanatomie und der Sensibilitätsleitung im Rückenmark und in der Medulla oblongata. Folia Neuro-biologica, Bd. ix., 1915, pp. 225–336.

Bruce, A.: A Topographic Atlas of the Spinal Cord. London, 1901. Distribution of the Cells in the Intermediolateral Tract of the Spinal Cord. Trans. Roy. Soc., Edinburgh, vol. xlv., 1906, pp. 105–131.

Bruce, A. N.: The Tract of Gowers. Quart. Journ. Exp. Physiol., vol. iii., 1910, pp. 391–407.

Coghill, G. E.: The Reaction to Tactile Stimuli and the Development of the Swimming Movement in Embryos of Diemyctylus torosus, Eschscholtz. Jour. Comp. Neur., vol. xix., 1909, pp. 83–105. The Primary Ventral Roots and Somatic Motor Column of Amblystoma. Jour. Comp. Neur., vol. xxiii., 1913, pp. 121–144. Correlated Anatomical and Physiological Studies of the Growth of the Nervous System of Amphibia. I. The afferent system of the trunk of Amblystoma. Jour. Comp. Neur., vol. xxiv., 1914, pp. 161–233.

Collins, J.: A Contribution to the Arrangement and Functions of the Cells of the Cervical Spinal Cord, to which is Appended a Note on Central Changes Secondary to Long-continued Disuse of One Extremity. New York Med. Journ., vol. lix., 1894, pp. 40–98.

Curtis, A. H. and Helmholz, H. F.: A Study of the Anterior Horn Cells of an Amelus and their Relation to the Development of the Extremities. Jour. Comp. Neur., vol. xxi., 1911, pp. 323–343.

Dogiel, A. S.: Der Bau der Spinalganglien des Menschen und der Säugetiere, Jena, G. Fischer, 1908, 151 pp., 14 plates.

Donaldson, H. H., and Davis, D. J.: A Description of Charts Showing the Areas of the Cross-sections of the Human Spinal Cord at the Level of Each Spinal Nerve. Jour. Comp. Neurol., vol. xiii., 1903, pp. 18–39.

Duret, H.: Sur la distribution des artères nourricières du bulbe rachidien. Arch. de Physiol. norm. et path., vol. v., pp. 97–114, 1873.

Fabritius, H.: Studien über die sensibele Leitung im menschlichen Rückenmark. Arbeiten a.d. Path. Inst. Univ. Helsingfors, Bd. ii., H. 1, 1908. Zur Frage nach der sensibelen Leitung im menschlichen Rückenmark. Monats. f. Psychiat. u. Neurol., Bd. xxxi., 1912.

Fabritius, H. and Berman, E. v.: Zur Kenntnis der Haut- und Tiefen- Sensibilität, untersucht mittels der Abschnürungsmethode. Pflüger's Archiv, Bd. cli., 1913, H. 4–6.

Foerster, O.: Die Indikationen und Erfolge der Resektion hinterer Rückenmarkswurzeln. Wiener klin. Wochenschr., 1912, No. 25.

von Frey, M.: Untersuchungen über die Sinnesfunctionen der menschlichen Haut. Abhangl. kgl. sächs. Gesellsch., Bd. xl., 1897 (Math.-Phys. Classe, Bd. xxiii.).

Van Gehuchten, A.: La moelle epinière des larves des batraciens (Salamandra maculosa). Arch. de Biol., t. 15, 1897.

Goldstein, K.: Ueber die aufsteigende Degeneration und Querschnittsunterbrechung des Rückenmarks (Tractus spinocerebellaris posterior, Tractus spino-olivaris, Tractus spinothalamicus). Neurol. Centralblatt, No. 17, 1910.

Harrison, R. G.: Further Experiments on the Development of Peripheral Nerves. Am. Jour. Anat., vol. v., 1906, pp. 121–131.

Head, H.: On Disturbances of Sensation with Especial Reference to the Pain of Visceral Disease. Brain, vol. xvi., 1893, pp. 1–133.

Head, H., Rivers, W. H. R. and Sherren, J.: The Afferent Nervous System from a new Aspect. Brain, vol. xxviii., 1905, pp. 99–115.

Head, H. and Thompson, T.: The Grouping of the Afferent Impulses within the Spinal Cord. Brain, vol. xxix., 1906, p. 537.

Herrick, C. Judson.: The Medulla Oblongata of Larval Amblystoma. Jour. Comp. Neur., vol. xxiv., 1914, pp. 343–427.

Herrick, C. Judson and Coghill, G. E.: The Development of Reflex Mechanisms in Amblystoma. Jour. Comp. Neur., vol. xxv., 1915, pp. 65–85.

Ingbert, C.: On the Number of the Medullated Nerve Fibers in the Dorsal Roots of the Spinal Nerves of Man. Jour. Comp. Neur., vol. xiii., 1903, pp. 53–120. On the Density of the Cutaneous Innervation in Man. Jour. Comp. Neur., vol. xiii., 1903, pp. 209–222. An Enumeration of the Medullated Nerve Fibers in the Ventral Roots of the Spinal Nerves of Man. Jour. Comp. Neur., vol. xiv., 1904, pp. 209–270.

Kadyi, I.: Ueber die Blutgefässe des menschlichen Rückenmarks, Lemberg, 1889. The Polish original appeared in 1886.

Keith, A.: The Growth of Brain in Men and Monkeys, with a Short Criticism of the Usual Method of Stating Brain Ratios. Journ. of Anat. and Physiol., vol. xxix., 1895, p. 297.

Key, E. A. H., and Retzius, G.: Studien in der Anatomie des Nerven-systems und des Bindegewebes, 1. Hälfte, Stockholm, 1875.

Kohnstamm, O.: Ueber die gekreuzt-aufsteigende Spinalbahn und ihre Beziehung zum Gowers'schen Strang. Neurol. Centralbl., 1900.

Kohnstamm, O. and Quensel, F.: Centrum Receptorium der Formatio reticularis und gekreuzt aufsteigende Bahn. Dtsch. Zeits. f. Nervenheilk., Bd. xxxviii., 1908.

Krause, R., and Aguerre, J.: Untersuchungen über den Bau des menschlichen Rückenmarkes mit besonderer Berücksichtigung der Neuroglia. Anat. Anz., Jena, Bd. xviii., 1900, pp. 239–252.

London, D. M. van: The Extent of the Sensory Disturbances in Tabes Dorsalis and its Significance in the Study of Segmentation. Folia Neurobiologica, Bd. iv., 1910.

Lüderitz, Carl: Ueber das Rückenmarkssegment. Arch. f. Anat. u. Physiol., 1881, Anat. Abt., S. 423–494.

May, W. Page: The Afferent Path (Review). Brain, vol. xxix., 1906.

Mies, J.: Ueber das Gewicht des Rückenmarkes. Centralb. f. Nervenheilk. u. Psychiat., Bd., xvi., 1893, p. 547.

Münzer, E. and Wiener, H.: Beiträge zur Analyse der Funktion der Rückenmarkshinterstränge. Neurol. Centralb., 1899. Experimentelle Beiträge zur Lehre von den endogenen Fasersystemen des Rückenmarkes. Monatschr. f. Psychiat. u. Neurol., Bd. xxviii., 1910.

Onuf, B., and Collins J.: Experimental Researches on the Localization of the Sympathetic Nerve in the Spinal Cord and Brain, and Contributions to its Physiology. Journ. of Nerv. and Ment. Dis., 1898, pp. 661–676.

Onuf, B. and Collins, J.: Experimental Researches on the Central Localization of the Sympathetic with a Critical Review of its Anatomy and Physiology. Archives of Neurology and Psychopathology, vol. iii., 1900, pp. 1–252.

Petrèn, K.: Ein Beitrag zur Frage vom Verlaufe der Bahnen der Hautsinne im Rückenmarke. Skandinavisch. Arch. f. Physiologie, Bd. xiii., 1902. Sur les voies de conduction de la sensibilité dans la moelle épinière. Revue Neurol., 1911.

Polimanti, O.: Contributi alla fisiologia del sistema nervoso centrale e del movimento dei pesci. Zool. Jahrb., Abt. f. Zool. u. Physiol., Bd. xxx., 1911, pp. 473–716.

Philippson, M.: L'autonomie et la centralisation dans le système nerveux des animaux, Paris, 1905.

Ranson, S. W.: Alterations in the Spinal Ganglion Cells following Neurotomy. Jour. Comp. Neur., vol. xix., 1909, pp. 125–153. Non-medullated Nerve Fibers in the Spinal Nerves. Am. Jour. Anat., vol. xii., 1911, p. 67.—The Structure of the Spinal Ganglia and of the Spinal Nerves. Jour. Comp. Neur., vol. xxii., 1912, pp. 159–175. The Course within the Spinal Cord of the Non-medullated Fibers of the Dorsal Roots: A Study of Lissauer's Tract in the Cat. Jour. Comp. Neur., vol. xv., 1913, pp. 259–281. The Tract of Lissauer and the Substantia gelatinosa Rolandi. Am. Jour. Anat., vol. xvi., 1914, pp. 97–126.

Ravenel, M.: Die Massverhaltnisse der Wirbelsäule und des Rückenmarkes beim Menschen. Ztschr. f. Anat. u. Entwickelungsgesch., Leipzig, Bd. ii., 1877, pp. 334–356.

Reid, R. W.: Relations between the Superficial Origins of the Spinal Nerves from the Spinal Cord and the Spinous Processes of the Vertebræ. Journ. Anat. and Physiol., London, vol. xxiii., 1888–89, pp. 341–353.

Rijnberk, G. van: Versuch einer Segmentalanatomie. Ergebnisse der Anatomie und Entw. (Merkel und Bonnet), Bd. xviii, 1910.

Rivers, W. H. R. and Head, H.: A Human Experiment in Nerve Division. Brain, vol. xxxi., 1908, p. 323.

Rothmann, M.: Ueber die Leitung der Sensibilität im Rückenmark. Berliner klin. Wochenschr., 1906, p. 47. Zur Frage der Sensibilitätsleitung im Rückenmark. Dtsch. Zeits. f. Nervenheilk., Bd. xliii., 1912, p. 433.

Schaffer, K.: Vergleichend-anatomische Untersuchungen über Rückenmarksfaserung. Arch. f. Mikr. Anat., Bd. xxxviii., 1891.

Sherrington, C. S.: Experiments in Examination of the Peripheral Distribution of the Fibers of the Posterior Roots of Some Spinal Nerves. Phil. Trans. Roy. Soc., London, vol. clxxxiv., 1893.

Sherrington, C. S.: The Integrative Action of the Nervous System, New York, 1906.

Singer, J., u. Münzer, E.: Beiträge zur Anatomie des Centralnervensystems insbesondere des Rückenmarkes. Denkschr. der Wiener Akad., Bd. lvii., 1890–1900, S. 569.

Steiner, J.: Die Functionen des Centralnervensystems und iher Phylogenese. I. Abteilung. Untersuchungen über die Physiologie

WELLCOME LIBRARY